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OPENING SPEECHES

ADDRESS BY THE PRESIDENT

EMERITUS PROFESSOR W. BROWN, F.R.S.

Ladies and Gentlemen,

It is with very great pleasure that I bid you welcome to these Jubilee Celebrations of the Association of Applied Biologists: I do this in the name and on behalf of the Council of the Association.

And now, before I proceed further, I have an important message to give you. A short time ago the Council sent the following message of loyalty to Her Majesty the Queen at Balmoral Castle:

> *TO THE QUEEN'S MOST EXCELLENT MAJESTY*
>
> *May it please your Majesty,*
>
> *On this the occasion of the fiftieth anniversary of the founding of the Association of Applied Biologists, we, the President, Council and Members of the Association convey to Your Majesty our humble duty and loyal greetings.*
>
> *W. Brown*
> *President,*
> *Association of Applied Biologists*
>
> *7th September* 1954.

and to-day we have had Her gracious reply, which I now read:

> *Please convey to the Council and Members of the Association of Applied Biologists my sincere thanks for their kind and loyal message. I send my best wishes for the Conference which is being held to celebrate the Jubilee of the Association.*
>
> *ELIZABETH R.*
>
> 13*th September* 1954.

You will all, I feel sure, join with the Council in expressing our great indebtedness to Her Majesty for sending us this message.

While we have with us a large representation of members and friends of the Association, both from home and abroad, we are particularly happy to welcome a number of distinguished visitors from overseas who have come to join us as official guests of the Association. Our guests are:

Dr P. BOVIEN, State Plant Pathological Institute, Lyngby, Denmark.
Prof. HANS BURSTRÖM, Botanical Laboratory, Lund University, Sweden.

Dr K. Starr Chester, Chief of Department of Agriculture and Biosciences, Battelle Memorial Institute, Columbus, Ohio, U.S.A.

Dr A. E. Dimond, Head of Department of Plant Pathology and Botany, Connecticut Agricultural Experiment Station, U.S.A.

Dr I. J. Doeksen, Central Institute for Agricultural Research, Wageningen, Holland.

Dr E. Gram, Director, State Plant Pathological Institute, Denmark.

Dr F. O. Holmes, Rockefeller Institute, New York, U.S.A.

Mr D. Hille Ris Lambers, Bennekom, Holland.

Dr H. Martin, Science Service Laboratory, London, Ontario, Canada.

Dr K. W. Neatby, Director, Science Service, Ottawa, Canada.

Prof. E. van Slogteren, Laboratory for Flower and Bulb Research, Lisse, Holland.

Prof. Emeritus E. C. Stakman, University of Minnesota, U.S.A.

Dr V. E. Wilkins, Director-General of European Plant Protection Organization, Paris.

It will, I am sure, be the wish of all members of the Association that I should express more particularly the great satisfaction and pleasure which we feel in having these gentlemen amongst us.

My functions this morning are essentially introductory, and I do not intend to stand long between you and the Inaugural Address. I merely wish to outline, very briefly, the series of events which has led up to the meetings which we are now attending; in other words, to recall a few of the more salient points in the history of the Association.

We are actually somewhat in advance of the clock in holding our Jubilee in this month of September, for it was not until 8 November 1904 that the Association came into being. The moving spirit in this was Mr W. Collinge of Birmingham University, and at a meeting in the rooms of the Linnean Society, presided over by the late Prof. F. V. Theobald, the Association was founded under the name of The Association of Economic Biologists. There were twenty-six founder members, including some names very notable in biological science—of whom I might mention two: Sir Arthur Shipley and Sir Ronald Ross. Of this pioneer group it is wonderful to relate that there is one, Mr Cecil Warburton of Cambridge, who has passed the century and is still with us. As Mr Warburton occupies the unique position of being our sole surviving Founder Member, it seemed very fitting to the Organizing Committee that a telegram should be sent to him from this meeting, conveying the good wishes of the Association on this Jubilee occasion.

In its early days the Association was peripatetic, having no specific headquarters. It was not until 1917 that it established itself in London, at the Imperial College of Science and Technology, South Kensington. Meetings at first were held somewhat erratically and did not exceed two per annum. Summarized accounts of these meetings were published in pamphlet form—entitled Proceedings—but only for a few years, as an arrangement was made whereby papers read before the Association, or a selection of them, and general matters of business were published in *The Journal of Economic Biology*, owned and edited by Mr Collinge. This rather anomalous position was corrected in 1914, when *The Annals of Applied Biology*, our official journal, first appeared; and it has continued without intermission ever since.

The Association made steady, though not rapid, progress up to the time of the First World War, and then came the difficult war period and especially the latter half of it. These difficulties continued through the first four or five years after 1918. It was at this time that Prof. W. B. Brierley played a most important part in bringing about a reorganization of the Association; and later he was responsible for an equally important and a more long-continued contribution to its welfare by undertaking the editorship of the *Annals*, a service which he gave to the Association for a quarter of a century (1921–45). Prof. Brierley unquestionably set the high standard of the content of the *Annals*, of which we are justifiably proud. It is most unfortunate that the present state of his health has prevented him from being with us to-day. Had it been otherwise, Prof. Brierley would have been the obvious choice for the position which I occupy in these celebrations. We consider that, his position in the Association being as I have stated, we should mark our appreciation of his eminent services to us by sending a telegram from this meeting, conveying our remembrances and best wishes.

From 1925 onwards the Association, and with it the *Annals*, has continued to expand and flourish. There was some hold-up during the Second World War but this was more than made good by great expansion afterwards. Its curve of growth continues to go up and up; its membership list is now close on 700. One might in fact say that its curve of growth is the least biological feature of this biological association, inasmuch as it still shows no sign of that tailing-off—that sigmoid effect—which we expect to find in biological growth curves. As it now stands the Association is unquestionably the most authoritative body in this country in applied biological research, more particularly in the fields of agriculture and horticulture, and the *Annals* has established itself as the most important journal.

And now we are on the point of entering our second half-century. In looking back over the past fifty years we consider that we are entitled to some measure of pride and satisfaction in the progress made. But nothing that is biological can remain static and still thrive. We look forward with hope and expectation to still greater advances in the future, and the presence of such a large gathering on this occasion is to us a matter for much self-congratulation and gives us great encouragement for the future.

Finally, Ladies and Gentlemen, let me express the personal wish that all of you will have a thoroughly interesting and enjoyable time in the varied programme set before us.

REPLY ON BEHALF OF THE VISITORS FROM NORTH AMERICA

By K. STARR CHESTER
Battelle Memorial Institute, Columbus, Ohio, U.S.A.

It is a privilege and an honour to express to you, members of the Association of Applied Biologists and your guests from the Old World, the appreciation of those of us from North America for this opportunity to meet with you. In these troubled days we can take hope for the future in the community of interests and understanding that this meeting affords. I have been asked in particular to convey to you greetings from the officers of the American Phytopathological Society who wish you every success as you extend your influence and programme into the future.

We from the New World have long admired the Association of Applied Biologists, your organization, your journal, and your symposia for exchange of ideas. We heartily congratulate you on fifty years of outstandingly productive activity, and we feel assured that as the Association moves forward to round out its first century of activity, the high standards of the Association and its contributions to biological science will be maintained or even surpassed.

We are deeply grateful for this opportunity to meet our European colleagues and to develop our understanding of one another's work with the thoroughness that can only result from the personal contacts made possible here. We look forward with great interest and pleasure, not only to the formal programme but also to the opportunities we will have to visit the institutions of biological research in the United Kingdom where so much excellent work has been done.

We sympathize deeply with the hardships, the privations, and the disruptions of your research, consequent on the war, and we admire the courageous and able way in which you have carried on and advanced to new achievements, despite all this.

We most cordially invite you to visit our research institutions in Canada and the United States and give us the opportunity to repay, in some measure, the hospitality being shown us here.

The theme of the conference affords an excellent opportunity to survey the achievements of fifty years and the gaps in our knowledge and techniques as well. Through awareness of these gaps, we may re-orient our research toward qualitative advances, toward the opening of new avenues of endeavour and not merely the refining of the old ones.

North America produces food in surplus. As North Americans, we can easily underestimate the requirements of the World for effective pest control. We hope to obtain a better understanding of the magnitude of this problem during the conference. As a result, we can more effectively join with our colleagues in the Free

World in striving toward a common goal: ever increasing the contributions of biology to the welfare of man.

The days of the ivory tower in biological research are passing. Our problems to-day are so complex that it is only through co-operative efforts that we can hope to advance. As in the physical sciences, the research team is replacing the gifted individualist in biological research. This implies a growing need for the personal contacts such as this conference affords. In that connexion, I should like to call your attention to the intimacy and amicability of relations between Canadian and United States applied biologists, where international teamwork is the rule rather than the exception. Our work has been very materially aided by those scientists who have left the United Kingdom to devote themselves to work in Canada, particularly in Canadian universities. Our science has been enriched and inspired by the contributions of such men as the late A. H. R. Buller and the late C. L. Huskins.

To some extent your investigations and ours are complementary. In England and other European countries, there has been, and fortunately continues to be, a particular stress on fundamental research, while our work has tended, in greater degree, to emphasize the application of basic discoveries to the needs of man. The case of penicillin is but one of many examples. This is a wholesome situation and one that again stresses the importance of conferences such as the present one.

But beyond these practical considerations, important as they may be to us as scientists, there is a deeper significance to such a meeting as this. As scientists we have a tradition of international understanding and fellowship that is lacking in many other elements of society. Especially now, we have a particular opportunity and responsibility for fostering the international understanding that, alone, can lead us back to world tranquillity. Meetings such as this do much to further that end.

It seems fitting to conclude these remarks by repeating the first message telegraphed from young America to old Europe over the first successful trans-Atlantic cable on 27 July 1866: 'Glory to God in the highest, and on earth peace, goodwill towards men'.

REPLY ON BEHALF OF THE VISITORS FROM CONTINENTAL EUROPE

By E. GRAM
State Plant Pathological Institute, Lyngby, Denmark

Opinions registered through the years, on the subject of international scientific conferences, range from a vague feeling of againstness to sweeping statements indicative of frustration. It may sound as trite as would a few remarks about the weather, but still, it is only fair to recall all we owe to such conferences—from the first time they gave the young student a chance to see the great scientists, names he once knew only from lectures and books. And what a sight it was—these old biologists! In spite of the postulate that the old men are no longer picturesque the younger generation certainly will make its observations, and have its fun, just as we did.

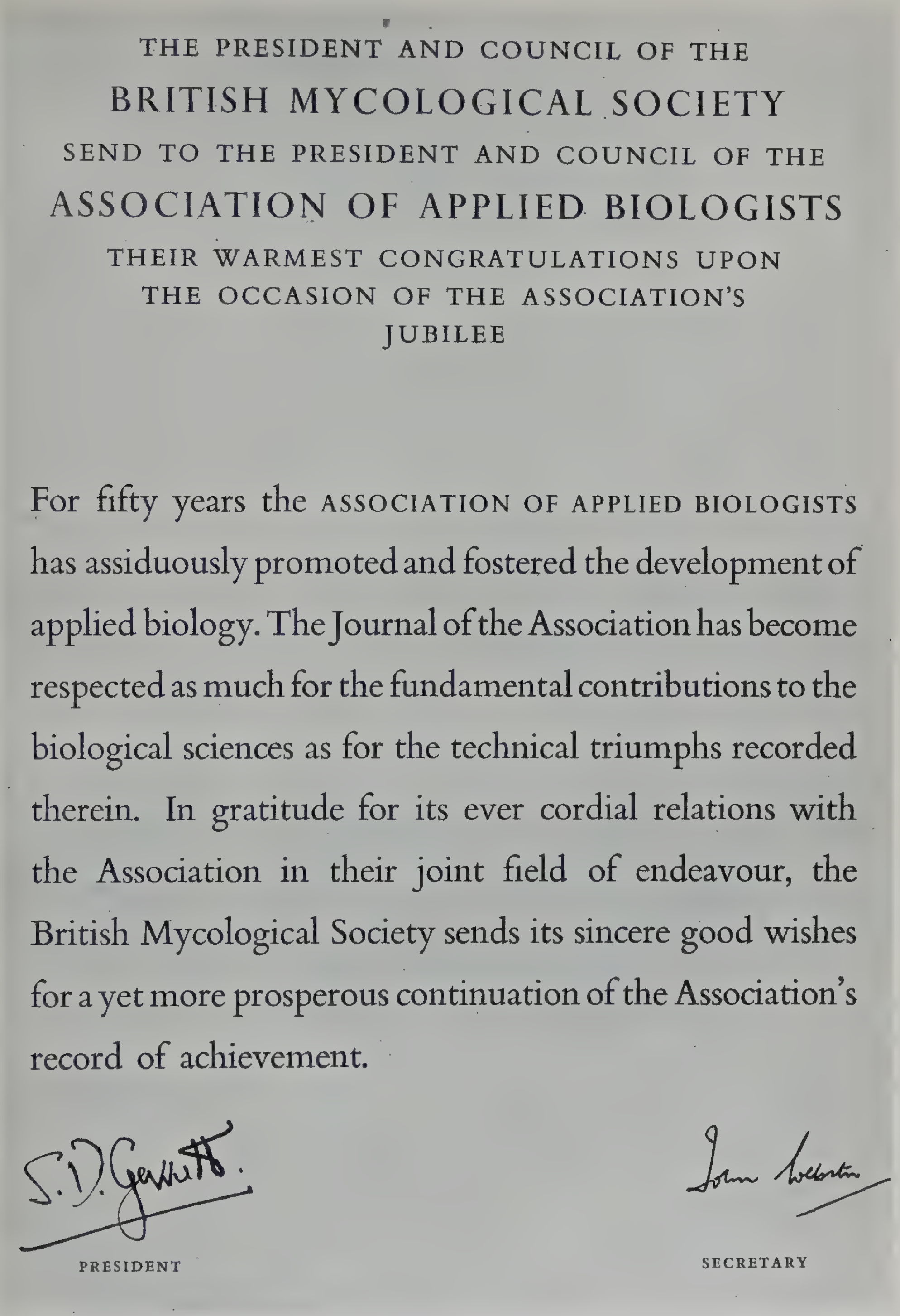
It so happens that the first international meeting to which I was delegated took place here in London. I owe to it the highly desirable lesson that a mountain may be climbed from several sides, that a fellow worker may have chosen an approach even more promising than your own. Personal feelings put aside I still maintain that it must be a very poor student who does not return from foreign laboratories with facts and ideas well worth his travelling expenses—even measured by the standards of the treasury's almost professional reluctance to part with its money.

When you British cross the sea you may meet a deeply rooted sense of realism; if you lay your course a little to the south the elegance of imaginative logic, or if you lay your course to the north a hard-working thoroughness. I need go no further; in a 3-dimensional system with realism, imagination, and thoroughness as its axes, you may find a place for all the European schools of science, as individualistic as they may be.—And when we from the continent come to Britain!...

Well, I must at once admit that I am biased. When I arrived at my university, intent on studying plant pathology, I was politely informed that this was outside—indeed beneath the curriculum. I fell back on mycology and several innocent fungi might have carried the burden of eighteen synonyms instead of seventeen, if, in 1914 I had not happened on the first numbers of *Annals of Applied Biology*, with papers on gooseberry mildew, the action of Bordeaux mixture on plants, bacterial diseases of fruit blossoms; with names, such as Barker, Gimingham, Salmon and Wiltshire, all new to me at that time.

I see before me the long row of stately volumes which have brought us inestimable wealth from far-reaching regions of science, even including, this year, good advice to speakers. When it says: Never drop the voice because you have come to a less important part of the paper—I might even stress the point, using the marginal note of one of our old reverends: Logic weak here, raise the voice!

When we from the continent come to Britain, we discover that the brevity of your papers is not due to lack of thoroughness, indeed, we owe you thanks because you do not burden your papers, and your readers, with all the details of the procedure. We learn to appreciate a type of logic wherein the picture, the contents, means more than the most elaborate of frames. Sometimes, when we see the first instalments of a new break-through we may mutter: Well, here is the aerial, but where in all the world is the earth? The Swedish author of *Everyman His Own Professor*, in his section on geometry, places all lines in two categories—straight and curved—'such lines as are neither straight nor curved are termed crooked'. We admire the British courage in selecting crooked lines as objects of study. Our original muttering turns to gratitude when the initial crooked line develops, e.g.



THE PRESIDENT AND COUNCIL OF THE
BRITISH MYCOLOGICAL SOCIETY
SEND TO THE PRESIDENT AND COUNCIL OF THE
ASSOCIATION OF APPLIED BIOLOGISTS
THEIR WARMEST CONGRATULATIONS UPON
THE OCCASION OF THE ASSOCIATION'S
JUBILEE

For fifty years the ASSOCIATION OF APPLIED BIOLOGISTS has assiduously promoted and fostered the development of applied biology. The Journal of the Association has become respected as much for the fundamental contributions to the biological sciences as for the technical triumphs recorded therein. In gratitude for its ever cordial relations with the Association in their joint field of endeavour, the British Mycological Society sends its sincere good wishes for a yet more prosperous continuation of the Association's record of achievement.

S. D. Garrett.
PRESIDENT

John Webster
SECRETARY

The Address presented on behalf of the British Mycological Society

(*Facing p.* 6)

into a means of transforming curves into straight lines, a method now in daily use in laboratories all over the world.

To many an old-time botanist or zoologist the foundation of the Association of Applied Biologists 50 years ago may have appeared rather absurd. But the words of SWIFT, 'how deserving are those who make two blades of grass grow where only one grew before', might be the motto of the Association. Everybody can see its merit now. I, therefore, need only express the congratulations from the continent in the form of a wish, that the rising curve of these 50 years may continue steadily upwards.

Russell, Sir E. John (1955). *Ann. appl. Biol.* **42**, 8–21

THE CHANGING PROBLEMS OF APPLIED BIOLOGY

By Sir E. JOHN RUSSELL

In addressing this distinguished scientific audience on this auspicious occasion I feel that I ought to begin by defining my terms. What exactly is Applied Biology? I have failed to discover any sufficiently precise form of words, and shall therefore, following high authority, evade the question and describe Applied Biology as the pursuit or avocation of the Applied Biologists: if a subject has been treated in the Association's Journal it comes within the description.

The subject is much older than the Association. Morton's *Cyclopedia of Agriculture*, published just on 100 years ago, has some remarkable articles showing how much shrewd observers of those days had discovered even with their primitive appliances. In dealing with plant diseases the Rev. M. J. Berkeley complained that 'the vegetable anatomist', as he called him, spent too much time indoors and too little in the field, in consequence though 'he may be able to describe with great accuracy and precision the various morbid appearances presented by any particular case, it is not likely that he should have any good general view of the subject. Vegetable pathology, therefore, presents us little more than a mass of facts of greater or less moment, out of which a clear and lucid system is still to be framed.'

That, then, was the problem as it appeared in 1855: the framing of a clear and lucid system out of a mass of facts of greater or less moment.

It was 40 years before much could be done, and then it came about by one of those curious accidents that have sometimes happened in the history of science in this country. In 1890 the Government, wishing to reduce the numbers of public houses, imposed on alcoholic drinks a tax the proceeds of which were to be used for the purchase and extinction of licences deemed redundant. The money was duly collected, but when the question of purchasing arose there was such a public outcry about handing it over to the owners of the licences—who were mostly brewers—that the plan had to be abandoned and the Government was left with some hundreds of thousands of £'s sterling for which there was no authorized purpose. In a listless and half empty Committee of the House of Commons Mr Arthur H. D. Acland proposed that the money should be used for technical education and this was accepted. Recognizing that for many counties this meant agricultural education and that very few teachers were available Viscount Chaplin wrote to the Chancellor of the University of Cambridge suggesting that it should undertake the task of training them. The University was not enthusiastic, but fortunately its Professor of Chemistry, G. D. Liveing, realized the importance of the matter, and in the Long Vacation of 1891 organized a voluntary class in Agricultural Chemistry—then regarded as covering all Agricultural Science. It was not a large class but it included

T. B. Wood, John Percival, Cecil Warburton and R. H. Adie, all of whom played a great part in subsequent developments.

At first University Extension lectures were given, but it was soon evident that more systematic teaching was needed. So in 1894 the County Councils of Kent and Surrey established the Agricultural College at Wye with A. D. Hall as Principal, John Percival as Botanist, and F. V. Theobald as Entomologist. Their function was to give systematic courses of lectures to students, to lecture on specific problems to farmers, and to give advice. They were primarily teachers: the Act made provision only for education, not research, and the coldly logical official mind sharply distinguished between the two. They took up the subject just about where the Rev. M. J. Berkeley had left it: out of a prodigious mass of empirical statements about the growing plant in health and disease, and some scientific observations of varying degrees of validity, they had to construct a subject that they could use for teaching students and advising farmers and gardeners. Gradually the subject took on a definite form and was made into a book. Percival published his *Agricultural Botany* in 1900: each successive edition was amended as the subject developed: many of the applied biologists of to-day were brought up on it. Theobald built up his subject of Agricultural Entomology: his book, *A Text-book of Agricultural Zoology*, came out in 1899*, but his task had been easier: Curtis had already in 1860 published his classical volume, *Farm Insects*, and Eleanor A. Ormerod's masterly *Manual of Injurious Insects* had appeared in 1892.

Cambridge did not at first take any direct part in the development of Applied Biology. R. H. Biffen, after graduating in 1896, joined a small expedition to Brazil, Mexico and the West Indies to study the sources of rubber: he was greatly impressed by the complete absence of any scientific direction in developing the immense natural resources of the tropics. On his return to Cambridge in 1898 he decided to make Economic Botany his life's work. But Cambridge had nothing in that line to offer, so he had to go back to Pure Botany. Not for long, however, for in 1899 the University Department of Agriculture was inaugurated and he was appointed to take charge of Agricultural Botany.

It was characteristic of these pioneers that their interests were very wide: they were naturalists in the old sense of the term. I have walked with Percival through meadows in which plovers were nesting and he was searching for their eggs, of which he was very fond. He knew just where the nests would be, and would run from one to another, while I, a mere chemist groping round, found nothing. Theobald dealt with the whole range of insects: the good and the bad in their setting in field, orchard, hop garden or market garden; he spent much time at the Natural History Museum sorting out mosquitoes, he also dealt with flies from India and much else: I have no idea how many new insects he described.† Biffen was a wonderful gardener, and though he had the distinction of never writing a book on his professed subject he did write one, and a very attractive one, on alpine plants for rock gardens.* It was indeed expected of a biologist in those days that he should know something or all about all living things: when H. H. King went out to the Sudan in 1906 as entomologist he found that his charges included hyenas and baboons.

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* In 1896 he had published a small book on *The Parasitic Diseases of Poultry*.

† C. A. W. Duffield (Wye College) in 1931 published a list of some 400 papers and books written by Theobald from 1885 onwards: the subjects included sponges, the Thrasher Shark, albino birds, but from 1894 onwards chiefly injurious insects.

The breadth of view of these pioneers had the advantage of enabling them to see the object of their study in its natural setting; it gave them something of the ecological view.

Besides their work in building up the subject, which was largely selective and descriptive, these pioneers had to advise farmers and gardeners how to deal with pests. A number of washes had already been discovered empirically or even accidentally: the classical example is the discovery of Bordeaux mixture in 1892. Other substances discovered empirically were lime, soft soap, paraffin, sulphur, lead arsenate, quassia and tobacco extract: but each grower had to make up his own mixtures—there were no proprietary articles—and there was no properly tested procedure. All sorts of mistakes were made: at times in preparing Bordeaux mixture ferrous sulphate would be used instead of copper sulphate because the trade name of the impure commercial salt was 'copperas'. H. H. Cousins, the chemist at Wye, in the 1890's standardized the paraffin wash, improving it by adding naphthalene. But he left England for Jamaica in 1900 and little chemical work was done on washes for the next seven years.

By 1904, when the Association was founded, vast amounts of empirical knowledge accumulated by generations of farmers and gardeners had been sorted out, tested and reduced to order; some scientific definition of the conditions necessary for healthy plant growth had been drawn up, and also descriptions of the common insect and fungus pests. The empirical methods of treatment had been stripped of much of their crudity, although little was known of the mode of action of either pests or washes.

The first volume of the *Journal of Economic Biology*, as it was then called, which began in November 1905 with Walter Collinge as editor (and also proprietor) is interesting as much for its advertisements and reviews as for its papers. Three reports on injurious insects in 1904 or 1905 were announced: a general one by Theobald, one on the Midland Counties by Collinge and one on Ireland by G. H. Carpenter. Watson's advertised a new microscope for highest power work, a first-class students microscope, for £6. 10*s*. 0*d*. The reviews were unblushingly candid: G. Massee's text-book on Fungi was 'nothing but a maze of words, without plan or cohesion, without aim or result'. As to another book, Collinge 'could not understand why the author had undertaken to compile it'. The Agricultural Colleges, or as he preferred to call them 'the so-called Agricultural Colleges', were 'with a few notable exceptions, badly equipped and staffed boys' schools undeserving of State or County Council Support'.

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* *The Auricula: the Story of a Florist's Flower.* Cambridge University Press, 1951 (published posthumously and edited by F. T. Brooks).

Up to this time the small band of agricultural entomologists and mycologists had concerned themselves mainly with the systematics and morphology of the insects and fungi concerned, but from about 1907 onwards they developed the second stage: the study of the life histories and the mode of life. Collinge emphasized the need for this in a lecture given at Bristol and printed in the second volume of the *Journal*. The need was widely recognized, but the workers were too few and their resources too meagre to enable them to get far. There were in those days no State grants for agricultural research and no research service: the work was mainly done by teachers in their spare time or by amateurs.

In 1910, however, the Development Commission was set up and for the first time Government grants were available for agricultural research. Staffs were increased and a new procedure became possible: joint work by men of different trainings. This enabled a new set of problems to be tackled and on a broader plan. Spencer Pickering, an amateur of ample private means, had studied Bordeaux mixture simply as a chemist and worked out a formula which seemed chemically better than any then current. It was tried in practice and proved no better than some of the older ones. But he had worked without help from a mycologist. B. T. P. Barker had for seven years been working almost single-handed at Long Ashton: he was now able to invite C. T. Gimingham, then a chemist, to join him, and working together on Bordeaux mixture they not only found the conditions for its optimum effectiveness but also showed its mode of action: something was secreted by the fungus which made the copper soluble so that it attacked and killed the fungus. The chemical technique of the time was not equal to the task of identifying the secretion: even now 30 years later the problem is not completely solved: Wain and Wilkinson have shown that some complex ion formation including amino-acid groups is involved.

Before the new research schemes got far, however, the 1914 war broke out. The food-production problems were mainly chemical and agricultural: only few biological problems were formulated. Three were serious. There was a terrible plague of houseflies in the army camps. Mechanization had not gone far: the Army depended on horses and mules. The manure heaps were usually stacked so near to the kitchens and mess huts that the flies could breed in the manure heaps, fly to the kitchens for food, and then to the mess huts for more. No good spray was available for some long time and the plague was appalling till F. W. Foreman and G. S. Graham-Smith devised a suitable spray.* A second problem had to do with wireworms. The food production programme required that three million acres of grassland should be ploughed up and planted with cereals and potatoes. But much of the grass was old and a heavy population of wireworms had developed: they badly attacked the crops and indeed probably caused as much loss of grain as the

* A mixture of coal tar creosote oil with bases from light oil. (*J. Hyg. Camb.*, 1917, 16, 109.)

German submarines. No effective way of dealing with them was found. Greater success was attained with the control of insect pests in food stores; J. W. Munro at the Imperial College did valuable work on this subject.

After the war more Government funds were available for research: in 1921 the farmers asked that £1,000,000 should be devoted to agricultural research as a solatium for the Government's professed inability to pay for the wheat they had grown, and for which they had been promised a satisfactory price—a request that would have been unthinkable 20 years earlier. The great industrial groups established their own research organizations: research was in short very much in the air and the universities, quick to sense the change, instituted the Ph.D. Degree to encourage post-graduate training—and incidentally it enabled a lot of dull but necessary research to be done cheaply. Two new industries developed: synthetic organic chemistry and scientific instrument making, both German monopolies before the war but now established here. These enormously increased facilities created a vast array of problems in applied biology—not on the principle of the plumber making work for somebody else, but because they were providing new tools and opening up vistas undreamed of by the older workers. The Association was not at first able to do much, having fallen on evil days during the war, but W. B. Brierley performed prodigies of labours in resuscitating the Association, and with the Imperial College group under the distinguished leadership of our President and of Lefroy set the subject going. In the ensuing developments two subjects have already had a marked influence: mathematical statistics and organic chemistry, and a third, atomic physics, seems equally promising: it has already given us the electron microscope, the tracer elements used in studies of herbicides, fungicides and virus diseases; and powerful radiations used by plant breeders. The effect of mathematical statistics is likely to be profound. It always marks an important stage in the development of a subject when quantitative conceptions begin to replace the rather vague generalizations based on experience. Rothamsted can fairly claim the credit of having introduced mathematical statistics into applied biology. R. A. Fisher devised the procedure. C. B. Williams realized at once the significance of these new concepts; he summarized his views of their importance in ecological studies in his interesting Presidential Address to the Ecological Society last year. He used them in his studies of the influence of weather conditions on the fluctuations of numbers of the different members of the insect population as sampled by his light trap, deduced some regressions showing the relations between the weather conditions at a given time and the numbers of a given insect at a later date: one of the purposes being to give a quantitative basis for forecasting infestations.* H. F. Barnes used statistical methods in his studies of fluctuations in numbers of wheat-blossom midges as did C. G. Johnson in studying those of the bean aphis. So also did R. W. Howe of the Pest Infestation Laboratory for investigating the rates of increase and decrease of insect populations. I can only wish that Maldwyn Davies of Bangor had lived long enough to put on a sound statistical basis his careful studies of the migratory movements of the aphid vectors of potato virus diseases, and the consequent spread of the diseases in relation to the environmental conditions. An interesting statistical study of his results was made later on by L. Broadbent. Another example of statistical treatment is furnished by the wide application of the probit* method, developed by C. I. Bliss in collaboration with R. A. Fisher, for the quantitative assessment of the results of bioassay. Yet another example of their use is furnished by the investigations of C. Potter and E. M. Gillham on the effect of atmospheric environment before and after treatment on the toxicity to insects of contact poisons.

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* Williams also used the data for working out the relationships between the numbers of species of insects and the size of their populations: the relative numbers of species with different numbers of individuals formed a logarithmic series. With characteristic humour he further showed that the numbers of publications by biologists in a year, as indicated by the reviews of applied entomology and applied mycology, also fitted the same logarithmic series (*Annals of Eugenics*, 1944). The possible relations of these two sets of observations would form a fruitful subject for a student debating society.

But statistical treatment, however impressive it may look, cannot make bad observations into good ones; its value is limited absolutely by the validity of the primary data. Increasing accuracy in records is needed. The ordinary recorded weather data are inadequate where the relations of an insect and a crop are concerned: the microclimate within the crop has to be the basis. Sir David Brunt is of course the leading authority on this matter, and if the Association could persuade him to give them a discourse on this subject it would certainly attract wide attention. A. Beaumont's observations of the microclimate within the potato crop at the Seale-Hayne College over the 11 years 1929–39 led to the formulation of his rule which as further developed has greatly facilitated the forecasting of attacks of potato blight. L. Broadbent, at Rothamsted, made a detailed comparison lasting for 3 years of the screen readings and those taken in a potato crop; the differences were marked: on occasion the microclimate within the crop favoured aphid flight when the weather outside did not—an observation of considerable importance in connexion with the spread of potato-virus diseases. At Reading R. H. Stoughton is studying the microclimate within the canopy of the apple tree at different times of the year and under different weather conditions; and at Wye H. W. Miles and his colleagues are studying the microclimate in the root zone of young apple trees under different orchard environments.

Statistical methods provided a working solution of the wireworm problem in the last war. Six million acres of grass land had to be ploughed up—double the area of the first war. No soil insecticide was available, but methods of estimating the numbers of wireworms in an acre of land had been devised and observations assembled showing what crops could safely be grown within certain limits of population density. A proper survey was therefore made and it formed the basis of the cropping programme. The safe crops provided little nutrient for the wireworms and their numbers gradually fell: they were not this time a cause of serious loss, thanks to the work of the Applied Biologists in the Survey.

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* The word 'probit' is not, as might be supposed, a piece of bad Latin but a contraction of 'probability unit'.

From about 1946 onwards statistical methods have been increasingly used in Applied Biology, and it is certain that this will continue. They are specially valuable for sampling populations, for studying fluctuating quantities, for relating one set of observations with another wherever some quantitative estimate is possible, and for a variety of other problems. One can sympathize with those people who took up biology at school or college in the hope of getting out of mathematics and now find that they must come back to the subject, and with the editor of the *Annals* whose difficulties were pathetically noted in R. W. Marsh's Presidential Address last year. One can only adapt a famous line of Virgil: the Great Father himself didn't wish the applied biologist to have too easy a life.

Statistical treatment, however, does not solve all the problems. Applied biology is essentially a field subject and the observational method remains as its solid basis. This is well organized for assessment of certain plant diseases and the possibilities of forecasting the probability of future attacks. A. M. Massee's forecasts of insect attacks, based on observed changes in insect population, and broadcast to Kentish fruit growers, are well known. Assessment of loss caused by virus yellows of sugar beet has been studied at Rothamsted by Marion Watson, R. Hull and others. The Advisory plant pathologists distributed over the country report on the health of crops to the Ministry of Agriculture: in his Presidential Address for 1949 W. C. Moore reviewed the great mass of information thus accumulated. More recently, E. C. Large (*Ann. appl. Biol.* **40**, 594) described the way in which the method of forecasting attacks of potato blight to which I have already referred—observations that include a good deal of careful meteorological measurement—is being worked by collaboration between the Agricultural Branch of the Meteorological Office and the Advisory plant pathologists: he is dealing with this on 15 September.

There are great possibilities of organized observational studies of many kinds. The country is rich in amateur field naturalists, accessible through the local Natural History Societies which in turn are banded together in large Unions (South-Eastern Union, North-Western Union and we hope soon, the North-Eastern and South-Western Unions) and the School Nature Study Union and similar bodies, and as C. B. Williams found in his studies of butterfly migration, they can be very helpful. The new National Nature Reserves have been defined by their Director-General, Mr E. M. Nicholson, as not only living museums for the preservation of areas important for their types of plant and animal communities or for their geological or physiographical features, but also as open-air laboratories for research and observation: and they will afford unique opportunities of observing population equilibria in conditions where human activities are largely eliminated.

The prodigious developments in chemistry have had extraordinary repercussions in applied biology, the end of which no one can foresee. One of the earliest results was the more accurate specification of the washes for fruit trees. The rather indefinite sulphur washes and tar oils were put in order, and a reliable standardized technique for evaluating insecticidal performance was developed at Long Ashton and East Malling: for the first time also the manufacturers agreed in 1938 to a minimum specification below which they would not allow their preparations to fall.* The vegetable insecticides, derris, tephrosia and pyrethrum were studied from 1923 onwards by F. Tattersfield, in collaboration with an able group including W. A. Roach, J. T. Martin and C. Potter, using methods that kept abreast of developments in pure organic chemistry. The active principles were isolated and their constitutions determined, which not only made possible the assay of commercial samples but opened the way to the synthetic manufacture of the pyrethrin-like ester, allethrin. Pyrethrum is of special importance: during the last war, particularly during 1940–2, it was used successfully by C. Potter for killing moth larvae that had been destroying dried fruits in barges and warehouses and it was used also for spraying air-raid shelters and human beings. It has become an important crop on the European farms in Kenya and a research group has been set up to study the problems of its production.

The greatest of all these modern changes, however, has been the enormous development of synthetic chemical industry. It began before the last war, but has developed at an increasingly rapid rate. The late Sir Jack Drummond, then at Boots' chemical factory, once told me that if a substance could be prepared in the laboratory by no matter how complex a procedure it would only be a matter of months before it could be manufactured on the large scale if the need arose. This possibility raised a new set of problems in applied biology: how to estimate insecticidal and fungicidal effectiveness with sufficient accuracy to enable the chemist to work out their relations with chemical constitution. First Tattersfield's apparatus and now the Potter tower provided the estimates of insecticidal value; had their relations with chemical constitution proved simple it should have been possible to compose formulae to satisfy any desired toxicity requirement. This has not been achieved but much has been done. The early investigations of F. Tattersfield and A. W. Rymer Roberts published in 1920 gave the outline of a chemical pattern and as developed later by Tattersfield and C. T. Gimingham led to the introduction of 3-5-dinitro-*o*-cresol (DNC) as an insecticide. The almost limitless number of variations on any chemical type that can be synthesized means that the task of testing them is endless. This insecticide story is very fascinating: it has been set out with characteristic thoroughness by J. T. Martin in the very interesting volume prepared at Long Ashton to celebrate their Jubilee last year. C. T. Gimingham gave an earlier account in his Presidential address in 1940. The fine adjustments made possible by the almost infinite range of possible insecticides has necessitated a closer study of how precisely they act on the insect. They do not all act in the same way, and in consequence results obtained with one insect may not hold for another, and the order of toxicity of a series of insecticides may vary with the test insect. These rapid advances of synthetic chemistry are necessitating much fuller investigations of insect physiology.

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* Described by C. T. Gimingham (1940) in *Ann. appl. Biol.*, 27, 161.

Just as the benzene ring with its many substitutions is the basis of the insecticides so quinone is a basis for fungicides and the effect of substitutions has been studied at Long Ashton. Much other work has been done; it still remains a mystery why out of all the elements, sulphur, copper, mercury and the precious metals, gold, silver and platinum, should be so drastically potent. These fungicide problems were fully discussed by R. W. Marsh in his brilliant Fernhurst Lecture before the Royal Society of Arts last June.

Most dramatic possibilities may spring out from the systemic insecticides and fungicides now being prepared. Some of the systemic insecticides are based on alkyl substitution products of a pyrophosphoric acid nucleus. Some of them have the enormous advantage that they can be applied as capsules in the soil and so can be used in conditions where spraying is impracticable, e.g. in dealing with swollen shoot disease in cacao trees: these have to be grown in the forest to ensure proper shade conditions. The specification for a systemic agent is exacting: it must not only kill the pathogen but must be able to enter and move about in the plant without suffering too much decomposition, also it must not persist unduly in any part that is going to be eaten by men or animals. This adds to the complication of the problem, but also to the interest of the investigation.

For years the search for a soil insecticide capable of dealing effectively with wireworms had been in vain. In 1951, however, the Jealott's Hill group were able to announce that Gammexane, the gamma isomer of hexachlorcyclohexane, could do this: it is now used with great success. But the roots absorb some of it and the potatoes taste of it when they are cooked. It may be harmless but no one likes the taint. Two more recent products, Aldrin and Dieldrin, show promise of causing less taint.

There still remains the problem of dealing with soil nematodes. B. G. Peters has tested many substances that kill the free-living and plant parasitic forms, though none is yet available for commercial use. Cysts can be induced to hatch out by treatment with the exudate from potato roots. So far the Cambridge chemists have not identified the active principle: when they do so, if it can be made on a commercial scale, it may solve the problem. Two substances or groups of substances are involved, both specific in their action: one inducing encystation, the other enabling the nematode to enter the appropriate root. But the quantities concerned are very minute and this makes the problem of identification extremely difficult.

The fact that these new pesticides are single chemical substances suggests the possibility that their action might be intensified by small quantities of some other substance. This has been proved in the case of pyrethrum, derris and ryania. A scent manufacturer once told me that the fragrance of rose, violet and other scents was heightened by a trace of skatol, a most disgusting smelling stuff. But there is as yet no clue as to what chemical structure constitutes a synergist and for the present the search would be purely empirical.

The high efficiency of these new substances has raised some new problems. When DDT was first used in orchards in the eastern counties it did its job very satisfactorily. Unfortunately it also killed the predators of the fruit tree red spider mite, but not the mite itself, so that this multiplied and became a new pest. Parathion, an organic phosphorus compound, is highly toxic to aphids and red spider mites but it also kills predators, as Massee and Elsie Collyer have shown, so that a new pest population may be built up. The effect of the insecticide on the whole population has to be studied.

A new set of possibilities is being opened up by the studies of the antibiotics produced by certain fungi and actinomycetes. P. W. Brian and his colleagues at the Butterwick laboratories, Welwyn, who have done much to develop this new subject, have shown that one of them, *Alternaria solani*, responsible for early blight in potatoes, produces an acid which is highly phytotoxic, and another, griseofulvin, produced by soil organisms, has systemic fungicidal properties. Other workers have shown that *Botrytis* can be controlled microbiologically. H. G. Thornton and his colleagues have studied the antagonism between strains of the nodule organism of the Leguminosae. Knowing what wonders have been achieved by penicillin we are justified in hoping for a great deal of help from these antibiotics: in particular in dealing with some very troublesome root diseases, for unfortunately there is as yet no good soil fungicide. It will be interesting to hear what Drs Garrett and Rishbeth have to say on this question.

In few branches of applied biology has greater use been made of the new tools than in the study of the virus diseases. It is an enthralling subject and has attracted a brilliant group of workers able to take full advantage of all the facilities offered by modern science. Biochemistry has long been brought in to discover the chemical nature of the virus; and the electron microscope—that amazing but costly and temperamental appliance—has revealed something of its structure. The very skilful manipulation of Marion Watson has revealed much of the mode of transmission. It still remains to discover how the virus multiplies in the cell. We can only hope the combined ingenuity of F. C. Bawden, N. Pirie, Kenneth Smith and their teams will find the solution.

The best way of dealing with a disease, however, is not to get it, and although problems of resistance and avoidance do not figure largely in the *Annals* their importance is fully recognized. The technique of building up virus-free stocks of soft fruits has been highly developed at East Malling with valuable practical results. Virus-free stocks of potatoes have been built up by Dr Salaman of Cambridge. The effects of environmental and cultural condition on the incidence of disease of wheat have been studied by Mary D. Glynne, and those of planting date and manuring on the incidence of virus diseases in potatoes by L. Broadbent,

P. H. Gregory and T. W. Tinsley. Fuller knowledge of the mode of attack will certainly help in the avoidance.

The use by Marion Watson and H. L. Nixon of radioactive phosphorus to learn more about the feeding of aphids is interesting as an example of the use of a new technique as well as for its own results.

In the end close links have to be established with the plant physiologist on problems of avoidance and with the plant breeder on questions of resistance. The normal physiological conditions of healthy plants in the field are being elucidated by D. J. Watson and others. Normal plant nutrition does not apparently come within the scope of applied biology, but malnutrition does, and special interest attaches to the study of the trace elements begun in this country by Katherine Warington at Rothamsted, and now, greatly facilitated by improved technique, carried on at several other centres, notably Long Ashton. Brierley long ago pointed out that a plant becomes diseased only if it is at the stage when it can be attacked at the same time as the pathogen is at the stage when it can attack. If the two can be thrown out of step the plant escapes and also if by some cultural treatment it can acquire sufficient resistance. Many practical growers have succeeded in doing this to some extent and although they are often inclined to make rather a mystery of the matter there is much that they can teach which the scientist has not yet learned. Happily varieties resistant to some of the fungus diseases exist, but usually in wild forms; and by one of Nature's perversities, resistance is often tied up with commercial worthlessness: the plant breeder has to untie the bonds. We are fortunate in having with us Prof. Stakman, widely honoured for the great part he has played in dealing with the rusts of wheat. That great pioneer E. S. Salmon, famous for his studies of Downy Mildew and other diseases of hops, is still breeding varieties resistant to them. Plant breeders like plant pathologists are making use of the new atomic physics: Aberystwyth already has its radioactive cobalt unit for breaking up undesirable associations of characters and we may yet see the new radiation appliances coming into wider use in applied biology.

Another remarkable reaction of the prodigious development of pure and technological organic chemistry on applied biology has been in connexion with growth-promoting substances. As with many other subjects now prominent the beginnings go back to the early days of this century—to 1910 in fact—but development was very active from 1934 onwards when the Utrecht group isolated the first growth-promotor and showed it to be indolylacetic acid. The discovery was of profound scientific interest because it revealed for the first time the mechanism by which the changing activities of the plant's life are controlled, and it was of equal practical interest because it opened up the possibility of directing these changes ourselves, instead of waiting for the plant to do it. Hopes are encouraged by the fact that an almost unlimited range of substances can be synthesized of the general type of the plant hormones, each differing somewhat from the others but suggesting the possibility of graded action from inertness to super-activity. R. L. Wain and the

Agricultural Research Council Unit at Wye are studying this subject, and on 14 September he is giving an account of the mode of action as at present understood. Already some of these new directives are used in practice. The stimulation of root formation from cuttings and from leaves has become a standard procedure in horticulture. It is not yet universally applicable: vinegrowers would like to use it for speeding up the propagation of Phylloxera-resistant stocks but have not yet succeeded. Some effective method will certainly be needed if ever a strain of cacao tree is found or bred resistant to swollen shoot disease and possessing also the necessary commercial qualities. Multiplication will have to be on a prodigious scale. The change from vegetative shoots to flowering shoots, the setting in or delaying of flowering, the setting of fruit without the intervention of pollen, the hastening or retarding of fruiting, are all practised on the large scale by tomato and fruit growers. Hawaiian pineapple growers stagger their harvests to facilitate the work of the canning factories; other fruit growers do the same to effect better distribution of labour of harvesting and to avoid market gluts. Difficult problems still remain: the fruits may come deformed or of poor flavour; stone fruits cannot yet be induced to set, but we need not doubt that these troubles will be overcome in time. Long Ashton and East Malling have been particularly active in applying these methods to fruit trees; T. Swarbrick's work at Long Ashton started in 1941 has already given a method of control of preharvest drop which is now an established orchard practice. Some control of dormancy has been effected. Dormancy of stored roots and tubers can be prolonged and sprouting avoided; great quantities of potatoes and root crops are saved annually by this means. The more difficult problem of controlling dormancy of fruit trees so avoiding frost damage is not yet solved, but hope still remains.

When agricultural scientists first heard of these substances 20 years ago it was hoped that they might act as a kind of super-fertilizer, enabling plants to use 100% of the nutrients supplied in fertilizer instead of only the usual 25–50%. These hopes, however, were disappointed. The hormone before use had to be strengthened against bacterial decomposition by the introduction of chlorine atoms; and then by one of Nature's little ironies it acted so potently on the plant as to kill it. But the killing was selective: for each substance some species, notably cereals, escape damage and so the selective weed killers were developed. This has been one of the major applications of science to agricultural practice in modern times. Probably about half our cereal crops are sprayed: the saving of grain has been estimated at 3 cwt. per acre: if we accept this figure these weed destroyers save us some half million tons of grain a year. Wheat growers overseas quickly realized their value: on the Canadian prairies the second cereal crop after the fallow is normally sprayed to destroy the incoming weeds; notable increases in yields have been obtained. Over the various countries something like 100 million acres are sprayed annually. The manufacture of herbicides has become an important new chemical industry, happily largely in British hands. G. E. Blackman and a team at Oxford, and the Jealott's

Hill and Fernhurst workers are studying a number of the problems involved in their use.

These new substances: the new insecticides, fungicides, plant hormones, herbicides and others give great powers of control but they also raise a host of new problems. Lord Acton said long ago that 'Power corrupts'. He was talking about political matters: but his dictum would hold true for agriculturists also if these new powers led to any lowering of the standards of cultivation or of general watchfulness in the belief that the scientists' latest device would rectify the effects of the practical man's slackness. More serious, perhaps, are the possible unexpected consequences. Nature's population of plants, insects, and other small animals is very varied but some sort of mobile equilibrium has been established. These drastically potent new agents may disturb the equilibrium with consequences that cannot yet be fully foreseen. The Nature Conservancy and the Game Research Unit of I.C.I. are investigating the matter, and, as already suggested, the help of the great Natural History unions should be enlisted.

The great industrial developments of recent years have effected important changes in the organization of research. The research institutions established by the major industries besides dealing with specific problems of the industry make fundamental investigations of far reaching importance. Dr Holmes is dealing with this subject but I should like to take this opportunity of saying how much applied biology and agricultural science owe to research centres such as Jealott's Hill, Fernhurst and Welwyn. They have the advantage of supplies practically unlimited on the laboratory scale, and of an immense range of substances which workers in the ordinary research institutes have laboriously to make for themselves. As for apparatus and appliances, it always seems to us ordinary mortals (though we may see them through rosy spectacles) that they are in the embarrassing position of having nothing left to ask for.

We have indeed travelled a long way since those far-off days of simple facts and broad generalizations easily apprehended: when a pocket lens served for most purposes and a £6. 10*s*. 0*d*. Watson microscope was a possession to be proud of. Applied biology has now developed to such an unwieldy extent that no one man can master the whole of it. Specialization has become imperative, the problems are now so complex that no one subject even can usually solve them: the aid of mathematics, biochemistry, physics, or other science has to be invoked. Teamwork has therefore become essential, calling for special personal qualities on the part of the workers and a new type of direction: ability to see what specialists are needed to solve the problems, to induce them loyally to co-operate, and above all, power to extract from the higher financial authorities the ever increasing funds for the increasingly costly appliances needed. The early applied biologist was a sturdy individualist working single-handed, generally taking a broad view and seeing his object in its setting but not penetrating far. The modern applied biologist, on the other hand, is a specialist dependent for help on the statistician, the chemist, the physicist and others; he may not see his subject as a whole but he can probe far more deeply than was ever possible before. The modern danger is that the specialists may lose touch one with the other and the subject may end up as it began: in Rev. M. J. Berkeley's words of 100 years ago—as 'a mass of facts of greater or less moment, out of which a clear and lucid system is still to be framed'. The danger can be averted only by arranging regular meetings for the reading and discussion of papers and carefully planned conferences where subjects of special importance can be examined on broad lines. This has long been the work of the Association: its strength to-day is proof of its effectiveness in the past and a hopeful augury for its continued usefulness in the future.

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PROGRESS AND PROBLEMS IN PLANT PATHOLOGY

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(With Plates 2 and 3)

It is a deeply appreciated honour to talk at the Jubilee convention of the Association of Applied Biologists. It is a pleasure also, because it is always a privilege to talk about plant diseases, and because the Association and I are of almost exactly the same age, plus or minus about a quarter of a century. At least it is true that my interest in plant pathology began to sprout about the time the Association was born.

My first tremendous impression of the terrible devastation caused by plant disease was in the first week of August 1904, when I stooked about 200 acres of wheat almost completely ruined by stem rust. My most recent one was in the first week of August 1954, when I saw 2 million acres of durum almost completely ruined by stem rust and 10 million acres of bread wheat badly damaged by it.

In 1904 much was known about fungus pathogens, but very little was known about the bacteria and viruses that cause plant disease. In 1904 scarcely a dozen bacterial diseases were known; now at least 170 different species are known to attack 150 genera of plants belonging to fifty families. During the past half century more than 200 plant viruses have been discovered and studied on virtually all kinds of economic plants. Not only has a vast amount of empirical information been accumulated, but deeper understanding has been attained and far greater precision in methods of investigation have been developed.

Many concepts regarding fungus pathogens have been developed since 1904. It is true that there had been considerable experimentation, that emphasis was shifting from the descriptive and taxonomic phases to the dynamics of fungi and fungus diseases. Mistakes were made; the mycoplasm theory, adaptation, bridging hosts, certain ideas regarding predisposition and the nature of disease resistance have been discarded. But to-day there are organized bodies of knowledge regarding the genetics, the physiology, and the ecology of plant pathogens. Enough information has been obtained to develop new principles and to validate many hypotheses. Sound concepts have replaced many unsupported theories. We are beginning to understand plant pathogenic fungi.

There has been a great advance in knowledge regarding plant parasitic nematodes, and new ones are continually being found. Realization of the importance of this group of pathogens is somewhat tardy, but there are indications that they are beginning to receive the attention that they deserve.

The nature of many non-parasitic diseases has been elucidated. The role of industrial by-products and of micro-elements in the soil has been determined in many cases, and the way has been pointed to the investigation of other diseases that probably are due to similar causes. It was scarcely suspected in 1904 that a few parts per million of chemicals such as selenium could be deleterious to plants. Nor was it known that the addition of small amounts of boron, sulphur, manganese, copper, zinc and other chemicals could remedy many disease conditions that were completely baffling 50 years ago.

Not only has much been learned about the nature of plant pathogens and other causes of plant diseases, but also about the disease process and the factors affecting the development of epidemics. Much has been learned about the production, liberation, and dissemination of inoculum; about the phenomena of infection; and about the influence of environmental factors on disease development. The variability in varietal resistance due to biotypes and races within species of pathogens and to environmental factors that affect host-pathogen relationships has been thoroughly studied for many diseases.

A scientific basis has been laid for sensible and feasible plant quarantine regulations. Within the past few years many countries have adopted an international plant quarantine convention sponsored by the Food and Agriculture Organization of the United Nations. How much good quarantines have done is difficult to estimate. The devastating coffee rust has been kept out of the western hemisphere, the South American leaf disease of *Hevea* rubber has been kept out of the eastern hemisphere, and many other pathogens have been fairly well contained. Nevertheless, some destructive pathogens have been distributed by man, notably downy mildew of hops, the *Ceratostomella* wilt of elms, and the virus causing the tristeza disease of citrus. Quarantines still need to be improved.

The inspection and certification of seed and other propagative parts of plants have been of great value. The use of certified potatoes has often increased yields 25% or more, principally by reducing diseases caused by viruses and certain bacteria and fungi. The improvement in methods of detecting diseases, with consequent improvement of certified propagative materials, has been of inestimable benefit.

The use of fungicides has emerged from the patent medicine stage to a relatively precise art. The evolution from copper sulphate and formaldehyde to copper carbonate dusts, to organic mercurial dusts, and still others has made it possible to control more seed-borne diseases much more effectively and with far less danger of injury to crop plants. It is a fact that the use of formaldehyde as a seed disinfectant for wheat did much more harm than good under certain conditions and in certain areas as late as 1915. No longer is it necessary to kill half of the plants to prevent a disease. The use of appropriate seed disinfectants for maize in the northern United States often increases yields almost as much as hybrid corn. There has been similar improvement in chemical sprays and dusts. Bordeaux mixture still has its uses, but the substitution of commercial lime sulphur, self-boiled lime sulphur, wettable sulphur, and still other materials and formulations has increased the effectiveness of control and minimized spray injury on many kinds of plants. The substitution of wettable sulphur for the regular lime sulphur for the pre-ripening application in a small apple orchard in Minnesota increased the value of the apples $2500, according to the statement of the orchardist.

Despite disappointments, progress has been made in controlling many diseases by the use of resistant varieties. The sugar-beet industry was saved in some areas of the western United States by the development of varieties resistant to the curly top virus. Losses due to sugar-cane mosaic have been reduced, virus stunt of corn has been kept in check in some areas by selecting for resistance in the regular breeding procedures, and the ravages of the citrus tristeza virus have been reduced by using sweet-orange rather than sour-orange stocks in budding.

The bacterial fire blight of apples and pears has been partly controlled by substituting resistant or semi-resistant varieties for many of the very susceptible ones that were grown 50 years ago. Many Fusarial wilt diseases, such as flax wilt, water-melon wilt, tomato wilt, pea wilt, and cabbage yellows, are being controlled in varying degrees in North America by the use of resistant varieties. Some of the smuts of wheat and other small grains have been fairly well controlled in some areas of North America by resistant varieties or by the use of varieties that are resistant enough to make seed treatment effective. Even some of the cereal rusts and rusts of other crop plants have been controlled for certain periods of time and in some places by resistant varieties. Potatoes resistant to late blight have been developed, although the resistance in many cases has been temporary and local. But a combination of semi-resistant varieties and improved spraying has simplified the problem of controlling the disease in some important potato-growing areas.

Losses in harvested products during transportation and storage have been greatly reduced in many countries. In 1904, as an example, rots of oranges during shipment from California to the eastern seaboard of the United States often destroyed 25–50% of the fruit. There were similar losses in other perishable products. Science and technology have greatly reduced these losses. There still are important storage problems of many products. As an example, wheat and other small grains are likely to be generally infested with moulds of the *Aspergillus* and *Penicillium* group which remain dormant at relatively low moisture content. A fractional percentage increase in moisture, however, may permit them to grow and cause 'sick wheat'. With the basic facts now available, control becomes an engineering problem in large grain silos. Losses from sap stain and decay of wood and wood products have been reduced by 50 or 75% in the United States. Naturally decay-resistant woods are now almost unavailable, but the length of life of many kinds of timber and timber products has been increased at least 3–10 years by preservative treatments, even though losses still amount to about a third of a billion dollars a year.

Plant pathology has become a science during the lifetime of this Association. A vast store of knowledge regarding plant diseases has been accumulated and organized; valid principles and sound concepts have been developed, control measures have become more scientific, methods of investigation have been improved immeasurably. More rigid scientific criteria are applied and more quantitative data are obtained. Research is more basic. The science has necessarily been subdivided into special fields, and co-operation between groups of specialists has become necessary in investigating many complex problems.

But even at a jubilee celebration too much time should not be devoted to boasting about past progress. It could be a good lesson in humility to compare what has been accomplished with what might have been. We are still relatively ignorant about many destructive diseases and deplorably ineffective in controlling them. Stem rust of wheat and other small grains is an example.

The wheat stem rust epidemic of 1904 in the United States and Canada stimulated study of the rust and possible methods of control. A special varietal testing and breeding programme designed to find or produce resistant varieties of spring wheat was added by the U.S. Department of Agriculture to its wheat improvement programme in 1905 and has been carried on continuously and expanded periodically since that year. Canada also intensified the search for resistant varieties. The need was greatest in the hard-red spring-wheat region, Minnesota and the Dakotas in the United States and the prairie provinces of Canada, because the stem rust menace was greatest in that area.

Marquis wheat, produced at the Central Experimental Farm, Ottawa, Canada, and distributed in Canada in 1909 and shortly thereafter in the United States, seemed to have partly reduced the rust hazard, because it matured early enough to escape severe damage in some years and in some places. In 1916, however, a terrible epidemic swept over most of the spring wheat area and destroyed about 300 million bushels of wheat in the United States and Canada. For a distance of more than 600 miles from eastern Minnesota to eastern Montana I did not see a single normal wheat field, and most fields were not worth harvesting. Marquis succumbed along with the other varieties, because the rust epidemic struck with full intensity before even this early-ripening variety could mature. It was clear that an early variety could not always be depended on to win the annual race between wheat and rust.

The epidemic of 1916 had several far-reaching results. It bankrupted many spring-wheat growers; it caused the abandonment of wheat growing in parts of the hard-red spring-wheat region and hastened the movement toward diversified farming; it caused the substitution of rust-resistant durums for the susceptible bread wheats in large areas of the region; it led to the organization of nation-wide rust epidemiology studies; it stimulated the initiation of a national barberry eradication campaign and the amplification and intensification of breeding for rust resistance.

The first important result of expanded epidemiology studies was the discovery that *Puccinia graminis tritici*, one of the biologic forms described by Eriksson and Henning, comprised many forms or races. Theoretically it seemed that biologic forms which differed in ability to attack different kinds of cereals might comprise forms or races that differed also in virulence on varieties of the same kind of cereal. As the species *P. graminis* comprised one form, *tritici*, that could attack wheat and barley but not oats and rye, another, *avenae*, that could attack oats but not the other small grains, still another, *secalis*, that could attack rye and barley but not wheat and oats, why might not *tritici*, *avenae* and *secalis* comprise forms that differed in ability to attack different kinds of wheat, oats and rye, respectively?

In the late summer of 1916, therefore, rusted wheat and wild grasses were collected on a line westward from Minnesota to the Pacific coast. Several varieties of wheat were inoculated in the greenhouse with each collection. All collections from east of the Rocky Mountains looked alike on all varieties inoculated. But the first collection and all subsequent collections obtained west of the Continental divide were distinctly different from the eastern collections. They produced weak infection (type 2) on Marquis, Haynes, Preston and other varieties that were completely susceptible (type 4) to all eastern collections. Both groups produced normal infection on club wheat. As the western collections could attack the club wheats, *Triticum compactum*, but not the hard-red spring wheats of the *T. vulgare* group, the new rust was rather naïvely named *P. graminis tritici-compacti*. It was soon surmised, however, that the subforms within the form *tritici* might be too numerous to name, so they were numbered.

Since a form of wheat rust had been found to which hitherto susceptible varieties were resistant, it seemed probable that there might be forms also to which resistant varieties were susceptible. This proved to be true. The Kansas Experiment Station had selected three lines of hard-red winter wheat that seemed immune from stem rust. They were immune from the two known forms, but as early as 1917 collections were found in Kansas and Oklahoma to which they were completely susceptible. A systematic search was then made for additional differential varieties of wheat. Among several hundred tested, twelve seemed to be representative of the club wheats, bread wheats, durums, emmers and einkorn. They were therefore selected as the standard differentials. By 1922 at least thirty-seven forms of *P. graminis tritici* had been discovered and described. About 275 are now known, and indications are that there are an indefinite number. With obligate parasites, such as the rusts, the problem is to find suitable biologic indicators, differential varieties of host plants. Thirteen are now used, and more will be added.

The forms *tritici*, *avenae*, *secalis*, and others of Eriksson and Henning have been elevated to the rank of varieties because of convenience and because there are perceptible differences in the morphology of the spores; and the biotypes or groups of biotypes within these varieties are now most commonly designated as physiologic races.

Races were soon found within the *avenae* and *secalis* varieties, and they probably exist within the *phleipratensis*, *agrostidis*, and *poae* varieties also.

There are many patterns of rust development, and, after 37 years of study, new patterns are still emerging. Until recently almost all wheat in Mexico was fall sown, the seeding time being from late September to early January. Winter wheat is grown in the United States as far north as southern Minnesota and South

Dakota, the time of seeding ranging from early September in the north to October or early November in the south. Minnesota, the Dakotas, and Montana grow most of the high-quality hard-red spring wheat of the United States, and this type of wheat extends into the prairie provinces of Canada. Durum is concentrated in certain parts of this area. Spring wheat is sown from early April to late May, or even into June. Local harvest begins in late February in Mexico and continues into May. Texas wheat is mostly harvested in late May and early June, and the harvest is progressively later northward, extending into late August or early September in the far north. There is rust on growing wheat, barley, and susceptible wild grasses somewhere in the interior of North America throughout the year. What is its life cycle?

All applied biologists know that only the dicaryotic uredial stage of stem rust can propagate successive generations on grains and grasses. The telial stage develops as host plants ripen or conditions become otherwise unfavourable for the continued development of the uredial stage. The young teliospores are also dicaryotic, but the two nuclei fuse to form the diplophase prior to germination. On germination of the teliospores, the diploid nucleus undergoes meiosis, the sporidia are haploid, they infect the barberry, unisexual pycnia are formed, and when the pycniospores of opposite sex are brought together by insects or otherwise, the dicaryotic aecial stage is formed. The aeciospores infect only grains or grasses and produce the uredial stage, which can multiply in geometrical progression and produce astronomically large populations of spores within a few weeks.

The salient factors regarding the epidemiology of stem rust can be summarized as follows:

(1) The uredial stage, the only repeating stage, does not survive the winter north of Texas except very occasionally and locally. It does, however, survive regularly in most of the wheat-growing areas of central and northern Mexico and sometimes in certain areas of Texas.

(2) The uredial stage does not normally persist through the hot dry summers in the principal wheat-growing areas of Texas and northern Mexico, except occasionally in high mountain valleys of north-eastern Mexico. It develops on barley during the summer in central Mexico and in recent years on spring-sown wheat, which has partly replaced barley. For many years there was relatively little seasonal interchange of rust between central and northern Mexico, but in recent years there has been considerable interchange.

(3) As the teliospores lose their viability at high temperatures, the aecial stage develops on barberry regularly and abundantly in the United States only as far south as the 39th parallel, except in eastern and western mountain regions where high elevations substitute for northern latitudes. Certain native *Mahonias* in Mexico may also become infected at elevations of about 10,000 ft.

(4) The north and south are mutually complementary in stem rust development. Urediospores may be blown to the south in the fall, where the rust can become established and develop throughout the winter in the uredial stage. The rust may

then be blown northward the next spring and early summer and the rust extends northward in successive waves.

Observations prior to and during 1917 had incriminated the barberry as an early and prolific source of rust in the spring wheat region. An eradication campaign was therefore begun in North Dakota in 1917 and a national campaign was started early in 1918 in thirteen northern wheat-growing States. Although this action preceded comprehensive knowledge about rust epidemiology, it soon proved to be more fully justified than had been anticipated. Barberry bushes proved to be unexpectedly numerous in rural areas close to grain fields; they often rusted heavily in the spring, sometimes a month before the arrival of wind-blown spores from the south; numerous destructive local epidemics were studied, extending from a few rods to many miles from the bushes; and it became clear that many local epidemics might coalesce into general epidemics. Naturally, it was postulated that the barberry might also be the breeding ground for new races. The supposition was strengthened when more rust races were consistently found near the bushes than at a distance. Craigie's discovery of the sexual function of the pycnia made it possible to confirm experimentally the hypothesis that many new races arose by hybridization between existing races, that aeciospores and urediospores often were dicaryotic hybrids.

The importance of barberry eradication in the control of stem rust now became doubly clear. The barberry was the medium for the production of much rust and for many kinds of rust. It was the source of much inoculum and of many physiologic races. There are 70 billion (U.S. billion) aeciospores on a single large barberry bush at one time, and several crops may be formed. Assuming that 1 % caused infection on a susceptible host, with the formation of uredia within a week or 10 days, each containing 100,000 urediospores, a conservative figure, the progeny would be 7×10^{13}, 70 thousand billion urediospores. And these spores could be carried to a height of 10,000 ft. and for hundreds of miles by the wind. After all, when spores 30μ long are several thousand feet up in the air, they probably do not fall to earth; they must be carried down by rain or downward air currents. Rust can therefore spread either continuously or discontinuously from infection centres near barberry, or from any other infection centres.

The barberry eradication campaign has continued and expanded from 1918 to the present time. By 1941 296 million bushes had been destroyed on 126,000 properties. Assuming that each bush carried less than half of a heavy spore load, barberry eradication prevented the annual production of 9×10^{18}, or 9 quintillion aeciospores in the United States, enough to inoculate every acre of wheat in the United States and Mexico with 100 billion spores, with some to spare for Canada. The eradication at least delayed the onset of rust in the spring in the northern United States; it eliminated thousands of early infection centres; it prevented many local and some rather extensive epidemics; it resulted in practical control of rust in some localities; it reduced the danger of general epidemics, but did not eliminate them; and it reduced the number of physiologic races, thus extending the life span of certain resistant varieties. Unfortunately it has been impossible to eradicate all barberry bushes during the past 35 years, because they had escaped from cultivation and had become thoroughly and abundantly established as wild bushes in many extensive areas, and native *Berberis canadensis* is abundant in certain areas of eastern United States, and *B. fendleri* is abundant in restricted areas in the southern Rocky Mountain area. Both species are susceptible to rust. Moreover, a single bush may produce about 35,000 seeds, many of which can remain in the soil for several years before germinating, thus necessitating a war of attrition instead of quick annihilation.

Barberry eradication did not eliminate rust epidemics because rust can spread from Mexico, where there are varying numbers of urediospores throughout the year, to Texas, to Oklahoma, to Kansas, to Nebraska, to the Dakotas and on into Canada. During the first week of June 1925, as an example, there was rust on wheat as far north as central Kansas. For almost a week the wind swept northward at 17–26 miles an hour, carrying rust spores 600 miles northward on a front more than 400 miles wide, thus inoculating grain in an area of a quarter of a million square miles. It was calculated that in early June 1952 there were 4000 tons of urediospores (150 billion spores per pound) on 4 million acres of wheat in sixteen counties of northern Oklahoma and south-central Kansas. Winds carried the spores to Minnesota and the Dakotas where they were deposited at the rate of 3·5 million an acre in an area of 40 thousand square miles. On an acre of fairly heavily rusted wheat there are about 50 thousand billion spores. Small wonder that strong winds followed by heavy dews or rain terrify those who have known the red scourge of wheat. In 1954 spores were being deposited at the rate of 10 thousand to 50 thousand per square foot daily at certain places in North Dakota 6 weeks to 2 months before harvest.

Rust control requires barberry eradication to prevent early development of rust and reduction in the number of physiologic races; and it requires the breeding of resistant varieties. The durums, widely substituted for bread wheats in the spring wheat area after the epidemic of 1916, remained resistant until the advent of races 11, 17, 21 and 38. In 1928 the durums rusted more heavily than Marquis because of the prevalence of race 38 to which Marquis is resistant and the durums then grown are susceptible. In 1926, the resistant bread wheat variety Ceres (Marquis × Kota) was distributed by the North Dakota Experiment Station. It quickly became the most popular spring wheat because of its rust resistance and high quality. But in 1928 race 56, to which Ceres is susceptible, was first found near barberry in Iowa; it extended its geographic range, increased in prevalence, and was the most prevalent race by 1934. It caused a terrific epidemic on Ceres and other bread wheats that year and again in 1937. Ceres had served its term; it was no longer resistant.

But Thatcher was ready to come to the rescue. This double cross (Marquis × Iumillo) × (Marquis × Kanred) had some genes for generalized resistance from the Iumillo durum and genes from Kanred for immunity to some races. It was first distributed in small quantities by the Minnesota station and the U.S. Department of Agriculture in 1934, which was a non-rust year, and withstood the epidemic of 1935 in striking contrast to Ceres and other varieties. This spectacular debut stimulated rapid increase, which was accentuated still further when Thatcher survived the epidemic of 1937 in contrast to the other bread wheats, which were very severely injured. Very soon, however, Thatcher proved so susceptible to orange leaf rust and Fusarial head blight in the moister parts of Minnesota and the Dakotas that it yielded to other varieties. On upwards of 10 million acres in western Canada, however, with less leaf rust and head blight, it performed well until 1954 when it was severely damaged by leaf rust and by stem rust.

The varieties that replaced Thatcher in northern United States had the 'Hope type' of resistance. Hope and H44 resulted from a wide cross, Marquis × Jaroslav emmer; they were not suitable as commercial wheats, but had the emmer type of resistance to stem rust and certain other diseases. They were therefore crossed with a number of good bread wheats, and a plant breeding hope was realized. The rust resistance of Hope had been combined with good bread wheat quality in such varieties as Rival, Regent, Renown, Mida, Newthatch and others. True, there was complete linkage between factors for resistance to stem rust and susceptibility to bacterial black chaff and melanosis. Soon the durum varieties Stewart and Carleton (Mindum × Vernal emmer), which combined the macaroni quality of the first parent with the rust resistance of the second, replaced the susceptible durums. The golden age of spring wheat had begun. It lasted from 1938 through 1949, 12 years of immunity from epidemics of stem rust.

Barberry eradication and plant breeding seemed to have solved the stem rust problem in spring wheat. From 1938 to 1949, inclusive, only four races of stem rust, 17, 19, 38 and 56, were sufficiently prevalent to be important. They comprised more than 90% of all rust in the United States each year. And the spring wheats and the newer durums were resistant.

But in barberry areas of eastern United States the race situation was not so simple. Barberry was still perpetuating old races and spawning new ones. Some of these races could attack the emmers and consequently the resistant bread wheats and durums with the Hope or Vernal type of resistance. Among them was the very dangerous 15B, first found on barberry in Iowa in 1939. It had never become independent of barberry, however, and for a number of years was found only on or near barberry in the eastern States. Although it had made some threatening gestures, it always had subsided again. But in 1950 it exploded. It spread first into the Gulf States, then to Texas, thence northward in small quantities, and it finally ruined many late fields of durum and damaged some bread wheat in north-western Minnesota, North Dakota, and on into Manitoba.

Unusual weather favoured the establishment of race 15B in 1950. Much of the wheat in the north was 5 weeks later than normal, thus giving the relatively small amount of initial inoculum an unusually long time to multiply. The fall was unusually long, so that urediospores were exceptionally abundant on volunteer wheat and wild grasses in the north after winter wheat had become established southward. Then mass air movements carried clouds of spores into southern United States and Mexico, they caused widespread infection, the uredial stage survived the winter abundantly, and race 15B had become independent of the barberry. It now has double insurance for persistence: the uredial stage in the south and the aecial stage on remaining barberry in the north.

The rust problem had again become acute. Race 15B comprised 27% of all uredial isolates identified in the United States in 1950 and the percentages for the next 3 years were 41, 58, and 63. But, worse still, race 15B caused severe damage to all durum and bread wheat varieties that had been resistant in the spring wheat area. Losses in 1950 were heavy but localized; providential weather in 1952 reduced the severity of a threatening epidemic; but the percentage loss in 1953 and 1954 was extensive and severe as shown below:

	Percentage loss			
	Durum		Bread	
	1953	1954	1953	1954
Minnesota	75	80	10	15
North Dakota	65	80	30	35
South Dakota	80	75	35	20

Race 15B almost annihilated the durum crops in 1953 and 1954, and what durum there was in 1954 was very light and shrunken. The bread wheats of 1904 would have suffered the same fate as the durums of 1954. The bread wheats of to-day can also be destroyed, but not so easily as those of 50 years ago. It takes more rust, more time, and more favourable rust weather to destroy them. There has been a net gain even though it is not enough to insure against destruction when weather and other factors favour early and intense epidemics.

Breeding for resistance against 15B was begun shortly after its virulence became known. Certain Kenya wheats that had appeared to be resistant to 15B were widely used as parents in crosses in Mexico, United States and Canada. Almost as soon as an adequate sample of 15B became available for study, however, it appeared that it was not a single biotype but comprised a number that differed in pathogenicity on some varieties. As an example, seventeen isolates obtained in the regular physiologic race survey in the United States were selected for intensive study because there were indications of slight differences in virulence on the thirteen differential varieties used in the identification of races. These seventeen isolates were therefore tested on ninety-nine selected varieties of wheat and on a number of varieties of barley, and fourteen of the isolates proved different. It seems quite likely, therefore, that not only had increased amounts of 15B been produced in 1950 but that many different biotypes had also been produced. A second disconcerting fact is that some of the resistant Kenya varieties proved to be resistant only at moderate temperatures but completely susceptible at high temperatures.

There have been other changes in the prevalence of races. The variety Supremo, which had been highly resistant for a number of years in Mexico, succumbed completely to race 15B. Other varieties, however, had been produced by crossing certain Kenyas with varieties adapted to Mexican conditions. Among them were Kentana and Lerma. Under Mexican conditions they were generally resistant to race 15B, but in 1952 races 49 and 139, which had long been present in very small quantities in northern Mexico, increased greatly in prevalence because they were able to attack Kentana and Lerma at all temperatures that permit rust development. Thus the growing of varieties resistant to 15 B encouraged the increase of two races that had never been considered important. Another change took place in 1954. Races 29 and 48 A, long known but never before prevalent, increased greatly in prevalence in Mexico and the southern United States. They in turn attack certain varieties that are resistant to previously prevalent races. Thus the golden age, 1938 to 1949, is over; but greater effort than ever before is being exerted to create a new one.

The history of race 7 of oat stem rust parallels that of race 15 B. It was isolated from barberry or from the immediate vicinity of barberry for seven successive years prior to 1950, but in that year it exploded, as did race 15 B. It also attacks previously resistant varieties of oats. And 7 A became prevalent in 1954 and menaces certain resistant varieties, as does the virulent race 6, which is still restricted to barberry areas in the eastern United States.

Virtually all pathogens that have been adequately studied are now known to comprise large numbers of biotypes which are grouped into physiologic races by their effects on differential varieties of crop plants. Most species of plant pathogens are extremely complex. The extreme, as far as now known, appears to be *Ustilago zeae*, the common smut of corn. The progeny of two haploid sporidia were crossed 25 years ago, and at least 15,000 distinct biotypes have been produced from these two minute cells as a result of mutations and recombinations. The number is indefinite. At least a thousand biotypes of the root-rotting fungus, *Helminthosporium sativum*, have been studied at Minnesota. Flax rust, late blight of potatoes, the smut fungi, the mildews—all are complex and variable.

It is not easy to obtain and maintain varieties resistant to all the multitudinous races and biotypes of a single species of a pathogen. It is much more difficult to combine resistance to all important races of all important pathogens. And it is even more difficult to combine resistance to all races of all important pathogens with all of the desired plant characters and with quantity and quality of product. Genetic linkages between good and bad characters often are a formidable barrier. It may be necessary at times to sacrifice something to get something more important. It may be necessary to sacrifice colour of grain to get disease resistance. It may be necessary to sacrifice whiteness of flour and golden colour of macaroni in order to have bread and spaghetti. How hungry does a black-bean eater have to be before he will eat red beans, yellow beans, white beans or a mixture of the three?

There is evidence that atomic energy may be a very useful tool in inducing desirable mutants, including some that are disease resistant. Can it be used to break undesirable genetic linkages? Even more extensive trials than those now under way should be made.

Can nature put virulence into pathogens faster than man can put resistance into crop plants? If resistance lags behind virulence, will it become necessary to use

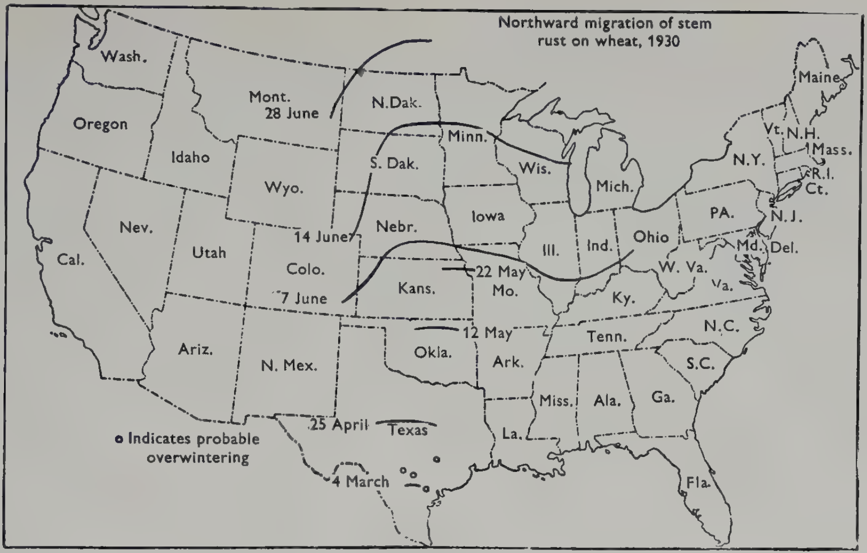

Northward migration of stem rust on wheat, 1930
Wash.
Oregon
Idaho
Mont.
28 June
N.Dak.
Minn.
Wis.
Mich.
Maine
Vt.
N.H.
Mass.
R.I.
Ct.
N.Y.
S. Dak.
Wyo.
Nev.
Cal.
Utah
14 June
Nebr.
Iowa
Ill.
Ind.
Ohio
PA.
N.J.
Md.
Del.
W. Va.
Va.
Colo.
7 June
Kans.
22 May
Mo.
Ky.
N.C.
12 May
Tenn.
S.C.
Ariz.
N. Mex.
Okla.
Ark.
Miss.
Ala.
Ga.
25 April
Texas
La.
Fla.
4 March
o Indicates probable overwintering

Fig. 1

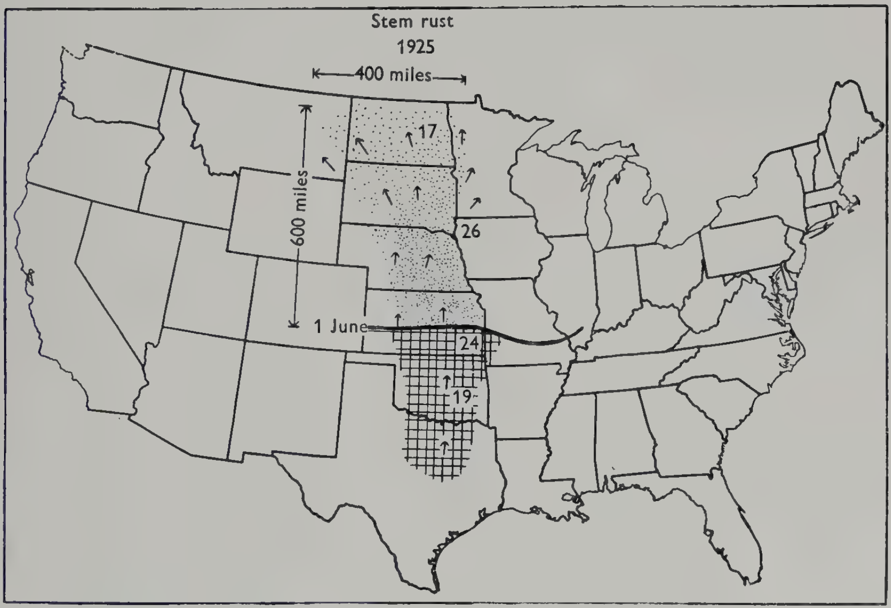
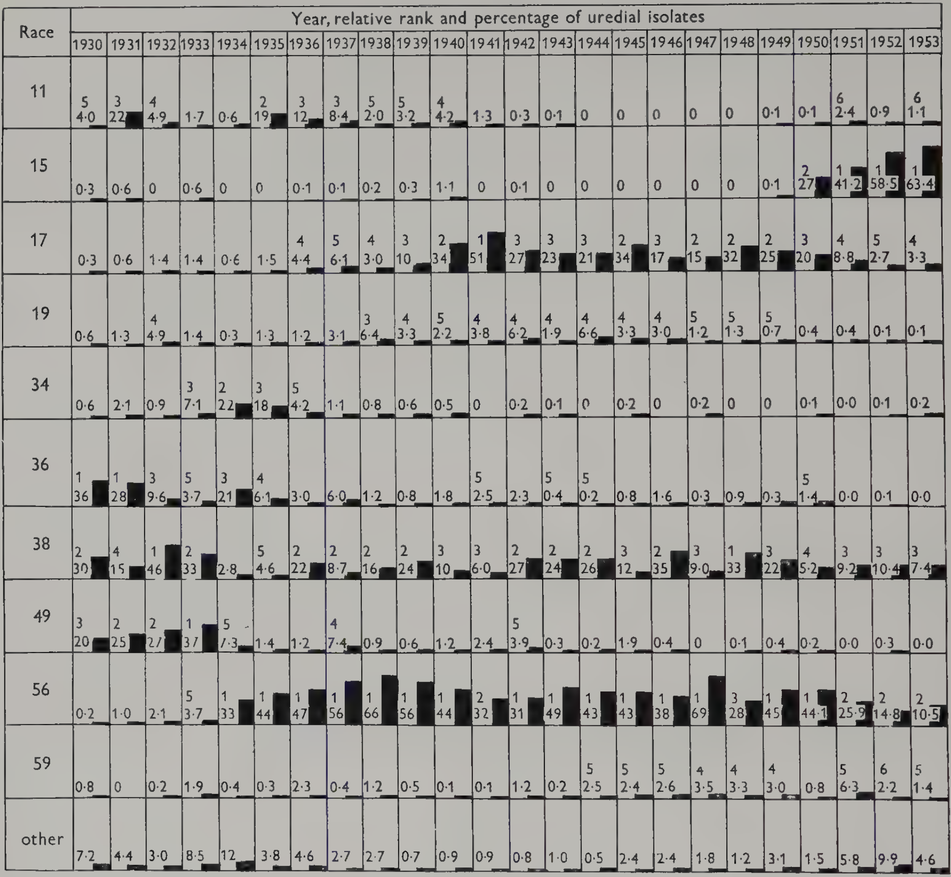

Stem rust
1925
400 miles
600 miles
17
26
1 June
24
19

Fig. 2

Race	L.C.	Ma.	Rel.	Ko.	Arn.	Mnd.	Spm.	Kub.	Ac.	Enk.	Ver.	Kpl.
56	●	●	●	●	○	○	○	●	●	○	○	○
17	●	●	○	●	●	●	●	●	●	●	○	○
19	●	○	○	●	●	●	●	●	●	●	○	○
38	●	○	●	●	●	●	●	●	●	●	○	○
15	●	●	●	●	●	●	●	●	●	●	●	○
189	●	●	●	●	●	●	●	●	●	●	●	●

● Susceptible ○ Resistant

Fig. 3



Race	Year, relative rank and percentage of uredial isolates																							
	1930	1931	1932	1933	1934	1935	1936	1937	1938	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953
11	5 4·0	3 22	4 4·9	1·7	0·6	2 19	3 12	3 8·4	5 2·0	5 3·2	4 4·2	1·3	0·3	0·1	0	0	0	0	0	0·1	0·1	6 2·4	0·9	6 1·1
15	0·3	0·6	0	0·6	0	0	0·1	0·1	0·2	0·3	1·1	0	0·1	0	0	0	0	0	0	0·1	2 27	1 41·2	1 58·5	1 63·4
17	0·3	0·6	1·4	1·4	0·6	1·5	4 4·4	5 6·1	4 3·0	3 10	2 34	1 51	3 27	3 23	3 21	2 34	3 17	2 15	2 32	2 25	3 20	4 8·8	5 2·7	4 3·3
19	0·6	1·3	4 4·9	1·4	0·3	1·3	1·2	3·1	3 6·4	4 3·3	5 2·2	4 3·8	4 6·2	4 1·9	4 6·6	4 3·3	4 3·0	5 1·2	5 1·3	5 0·7	0·4	0·4	0·1	0·1
34	0·6	2·1	0·9	3 7·1	2 22	3 18	5 4·2	1·1	0·8	0·6	0·5	0	0·2	0·1	0	0·2	0	0·2	0	0	0·1	0·0	0·1	0·2
36	1 36	1 28	3 9·6	5 3·7	3 21	4 6·1	3·0	6·0	1·2	0·8	1·8	5 2·5	2·3	5 0·4	5 0·2	0·8	1·6	0·3	0·9	0·3	5 1·4	0·0	0·1	0·0
38	2 30	4 15	1 46	2 33	2·8	5 4·6	2 22	2 8·7	2 16	2 24	3 10	3 6·0	2 27	2 24	2 26	3 12	2 35	3 9·0	1 33	3 22	4 5·2	3 9·2	3 10·4	3 7·4
49	3 20	2 25	2 27	1 37	5 7·3	1·4	1·2	4 7·4	0·9	0·6	1·2	2·4	5 3·9	0·3	0·2	1·9	0·4	0	0·1	0·4	0·2	0·0	0·3	0·0
56	0·2	1·0	2·1	5 3·7	1 33	1 44	1 47	1 56	1 66	1 56	1 44	2 32	1 31	1 49	1 43	1 43	1 38	1 69	3 28	1 45	1 44·1	2 25·9	2 14·8	2 10·5
59	0·8	0	0·2	1·9	0·4	0·3	2·3	0·4	1·2	0·5	0·1	0·1	1·2	0·2	5 2·5	5 2·4	5 2·6	4 3·5	4 3·3	4 3·0	0·8	5 6·3	6 2·2	5 1·4
other	7·2	4·4	3·0	8·5	12	3·8	4·6	2·7	2·7	0·7	0·9	0·9	0·8	1·0	0·5	2·4	2·4	1·8	1·2	3·1	1·5	5·8	9·9	4·6

Fig. 1

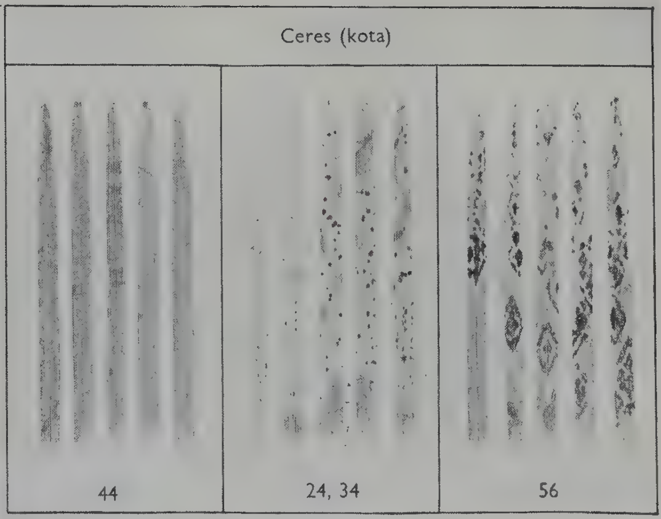


Fig. 2

STAKMAN—*Progress and problems in plant pathology* fungicides on extensive acreages of basic food crops that are subject to widespread epidemics? If so, can fungicides be developed that are effective in small quantities and that have therapeutic instead of merely preventive properties? Can systemic fungicides be developed? Can antibiotics be used effectively? Basic researches on an adequate scale are essential to find out.

Despite progress in understanding and controlling plant diseases during the past half century, far more research is needed. We still do not have the necessary breadth of vision and the depth of insight into plant disease problems. We need basic research to elucidate principles and practical experimentation to help alleviate situations. Immediate solutions must be sought for some of the most urgent problems. Much work must be practical, but basic research is likely to be the most practical in the long run, even in many fields of applied biology. A synergism is needed between the motivating forces of curiosity and the urge to solve problems. 'Research is the living source of progress' has proved to be even more true than when it was written. Appreciation of the value of research and facilities for doing it are still deplorably inadequate even in some of the most scientifically advanced countries.

The statement of the philosopher to the effect that science accumulates huge masses of data in attempting to expand the area of the known but succeeds only in expanding the area of the unknown should be amended to read: the more we learn the more we know how much more we want to learn to satisfy curiosity and the better we know how much more we need to learn to solve problems. At least we have learned in many fields of applied biology what it is that we want to know and what it is that we need to know. And even that is scientific progress.

Plant pathology has been intensely interesting and progressively productive during the life of this Association. Therefore I hope that 50 years hence I may again have the privilege of talking, to the text: Progress in plant pathology during the past 100 years and promises for the next 100.

EXPLANATIONS OF PLATES 2 AND 3

Plate 2

Fig. 1. The movement of stem rust northward from Texas to Canada in six successive waves from 4 March to 28 June 1930.

Fig. 2. The dissemination of stem rust over a quarter of a million square miles in the first week of June 1925.

Fig. 3. Reaction of twelve differential wheat varieties to six races of wheat stem rust. Races are identified by their effects on these and certain other varieties.

Plate 3

Fig. 1. The relative prevalence of physiologic races of wheat stem rust in the United States from 1930 to 1953, based on the identification of 500 to more than 1000 collections each year.

Fig. 2. Why race 56 ended the career of Ceres wheat. Ceres is virtually immune from race 44, extremely resistant to race 24, slightly less resistant to race 34, and completely susceptible to race 56.

Wigglesworth, V. B. (1955). *Ann. appl. Biol.* **42**, 34–44

THE CONTRIBUTION OF PURE SCIENCE TO APPLIED BIOLOGY

By V. B. WIGGLESWORTH

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During the Second World War many biologists, who had hitherto been concerned only in carrying out investigations in pure science, were given the opportunity of directing their talents to the solution of immediately practical problems. Many turned to this new field of endeavour with supreme self-confidence—well knowing that applied science was just like pure science, only rather easier. For many it proved a humbling experience. In the pure science to which they were accustomed, if they were unable to solve problem *A* they could turn to problem *B*, and while studying this with perhaps small prospect of success they might suddenly come across a clue to the solution of problem *C*. But now they must find a solution to problem *A*, and problem *A* alone, and there was no escape. Furthermore, there proved to be tiresome and unexpected rules which made the game quite unnecessarily difficult: some solutions were barred because there was not enough of the raw material available; others were barred because the materials required were too costly; and yet others were excluded because they might constitute a danger to human life or health. In short, they made the discovery that applied biology is not 'biology for the less intelligent', it is a totally different subject requiring a totally different attitude of mind.

In this lecture I propose to consider the relation between the two. I shall interpret the title, 'The Contribution of Pure Science to Applied Biology', in an algebraic sense—for, as we shall see, the contribution has often been the other way round. But first I must say a few words on the methods of science.

The methods of science

New knowledge in science comes in many diverse ways, but in so far as the deliberate search for knowledge is concerned it is customary to recognize two quite different procedures. There is first that formulated by Francis Bacon and called by him the 'Novum Organum'. This consists in the accumulation of facts which, it is anticipated, will eventually all fall into place; and without the exercise of any more thought than that required by a committee, a complete understanding of nature will be achieved. This method still has its advocates and its practitioners but it has always proved singularly unproductive.

The second method is the experimental method. This has often been described, perhaps nowhere better than by Claude Bernard a century ago in his *Experimental Medicine*. It consists in the formulation of an hypothesis which the investigator then attempts to prove, that is, to demolish, by a series of experiments. If all attempts fail the hypothesis is provisionally accepted as a theory or base for further hypotheses; and thus the provisional edifice of scientific knowledge is gradually built up.

The essential ingredient is the hypothesis. Where does this come from? It comes, of course, from the imagination which formulates ideas. Claude Bernard describes graphically how the investigator outside the laboratory should allow his imagination full rein; but when he enters the laboratory he should shed his imagination like his overcoat. We all recognize that the progress of science is constantly dependent on improved techniques. But technique alone is not enough. (One has only to contemplate the wasted effort that can be expended on new techniques just because they are new, such as the use of radioactive tracers in biology.) When we say that we lack a knowledge of techniques, as often as not we mean that we lack ideas.

Where then do the ideas come from that form the basis of these precious hypotheses? They come by thought. But thought is a difficult and painful process: most people would rather die than think; and that is why they are so ready to escape the necessity by adopting empiricism, or Baconianism—which sometimes appears in modern dress as the substitution of statistics for thought. But in scientific research there is no substitute for thought. That is not a truth which we readily admit. We are glad enough to extol the merits of teamwork, to demand heavier endowments for research, and to admire fine equipment, but we are reluctant to speak of the necessity for thought and the generation of ideas.

THE IMPACT OF PRACTICE ON SCIENCE

But where do thoughts come from? To conceive good thoughts you need a good brain, and a good brain prepared by education and experience to associate ideas and derive new conclusions from diverse observations. But even the best brains do not operate in a vacuum. They are subject to the influence of fashion. In science they may be led by fashion to pursue particular lines of study until these have become more and more specialized and less and less productive of important results. Take the examples of muscular contraction or nerve conduction, both fields of research which have engaged the attention of highly specialized schools of physiologists for many years. From time to time these schools have looked like becoming so specialized as to produce results which none but their own members could understand. But always the subject has been revivified by ideas from outside. At the present time, with techniques and ideas coming from physical chemistry, biochemistry, nuclear physics, X-ray crystallography, electron optics, these subjects are once more in a most exciting phase of eruption.

Now one of the most efficient correctives to the dangers of over-specialization is provided by the stimulus of contact with practice. The research worker in pure science who has reached the point where his ideas are going round and round in circles like a bee in a bell-jar, may have a new direction and stimulus given to his work by contact with some practical problem. One is tempted to borrow the jargon of the dialectical materialists and claim that the interaction of the opposites of theory and practice, of pure and applied science, is one of the most potent dialectics in the advancement of knowledge.

The zoologist studying the natural history or autecology of an animal is generally satisfied with a comparatively superficial knowledge of it. After all, there are so many animals in the world to know about. But when the applied biologist is confronted with some animal in competition with man—a mosquito carrying yellow fever or malaria, a migratory locust, an aphid bringing virus diseases to the potato crop—he requires a depth of knowledge of quite a different order. It is in these fields that the principles of ecology are being hammered out. It is a question of personal preference whether we regard this as an example of the pure science of ecology coming to the rescue of the applied biologist or as an example of the applied biologist showing how ecology should be studied.

We see the same state of affairs in taxonomy. Taxonomy provides the essential basis of any work to do with living creatures; and that, of course, is the real justification for the existence of our museum staffs. But museum workers were slow to appreciate the full implications of Darwinism. Although the principle of evolution was soon accepted, the museum worker, almost of necessity and by the very nature of his work, has clung to the idea of the fixity of species. During the last fifty years the development of genetics and ecology has been changing that, and to-day we hear much of the 'new systematics'. But what is not always appreciated is the contribution of the applied biologist to this change in outlook. The museum worker has long recognized geographical races; but it has been the applied biologist, looking at his animals in nature, at all stages in their development, far more intimately than the museum worker could possibly do, who has realized that a single species may present a variety of 'biological races' differentiated by their ways of life. Although it is requiring the painstaking work of the geneticist to analyse the nature of biological races and their relation to species formation, I do not think it would be an exaggeration to say that the discovery of these races was due to the applied biologist.

I have spoken of the need for thought, but one of the dangers by which science is beset is too much thought: an undue faith in the capacity of reason. For hundreds of years the great physicians of Europe based their medical practice upon systems of medicine which had been arrived at by a process of pure thought. And scarcely a vestige of these systems has remained: the purely rational process has indeed proved extraordinarily unproductive.

On the other hand, the scientific method has proved so amazingly successful during the past century or two that in these days reliance on pure reason is at a discount. Yet the risk of science, or parts of science, becoming enmeshed in some fabric of logic is by no means negligible. If one were to search the annals of current science I do not doubt that one would find small islands of scholasticism where existing theories are considered self-sufficient and the mind is satisfied with formal explanations in terms of these accepted theories. But the cold rude breath of experimental science blows everywhere and these sheltered corners do not remain undisturbed for long.

Traditional knowledge and empiricism

In the past, in the absence of that organized body of fact and theory that we call science, no discovery had permanence unless it was incorporated into the traditional procedures and some practical art. And since it is very difficult to be sure whether a given change in the practice of an art represents progress or decay the practitioners of such arts have always been extremely conservative. Indeed such a system of knowledge could remain stable only so long as it was intensely conservative.

Science has changed all that. A body of classified knowledge is being built up, held together and summarized by laws and theories which make possible an almost infinite number of predictions from a minimum of brief generalizations. We professional scientists know that all these generalizations are only provisional. They represent summaries of current opinion, some of which may endure for a thousand years or more, like the Ptolemaic conception of the universe; others may last a century or two like the system of Copernicus, Galileo and Newton; while yet others, which you and I formulate, are destined to be current for no more than a few years at the most.

But the general public does not know this. It is no wonder that the practitioners of crafts of every kind have come to rely more and more on science and have developed a flattering faith in the opinions of the scientist. On the whole I believe that faith is well founded; but there have been many examples, in the recent history of science, of scientists discrediting most valuable discoveries and beliefs through the inadequacy of the knowledge and the methods available to the science of the day.

There had long been a belief that fleas were connected with human plague; but when plague first appeared in India in 1896 and a strong scientific commission was appointed to investigate the matter they wrote in their report that 'the theory that plague is carried to man by some biting insect is scarcely worthy of statement'. When my father was a medical student he was taught that one Steinhaeuser had claimed that rickets could be cured by the administration of cod-liver oil—but that, in fact, chemists had shown that cod-liver oil contained only the same sorts of fatty acids as olive oil, and since olive oil was much pleasanter to take it was just as well to prescribe that!

In medical practice the fungus-infected rye grains known as ergot have long been used to induce prolonged contraction of the uterus and so to control post-partum haemorrhage. At one time this action was attributed to certain alkaloids present in the drug. But when I was a medical student I was taught that none of the characteristic alkaloids of ergot had this effect, and that any prolonged action of this kind upon smooth muscle which might be claimed by the doctors was simply due to the putrefactive bases, notably tyramine, which developed in the decomposing fungus. However, practising doctors, influenced I am afraid by an obstinate empiricism, continued to use extract of ergot for the treatment of post-partum haemorrhage, and this preparation continued to appear in the British Pharmacopoeia. Indeed, it was not until 1935 that Chassor Moir and Dudley reported that the watery extract of ergot did in fact contain an alkaloid ergometrine which had been overlooked by earlier workers, and that this alkaloid had just the properties for which the obstetricians had been using the drug for a century or more.

All this is not intended to depreciate the contribution of science to the practical arts but to illustrate the nature of that contribution. So very often it is not to *discover* some phenomenon of practical use, but ultimately (and sometimes long after that use has been adopted on purely empirical grounds) to provide a rational explanation for it. I submit that such rationalization is of the highest importance, for the two reasons I have already stated. First, because it gives stability and permanence to knowledge. Secondly, because there is a limit to the amount of empirical knowledge which the mind can retain; when that knowledge has been given a rational basis it will appear as the necessary consequence of natural laws, and a few general laws may be sufficient to predict an infinite number of special properties. One has only to think of the predictions that are possible in organic chemistry with the aid of a comparatively limited number of general principles.

EMPIRICISM OR DIRECT EXPERIMENT

When the scientific method is brought to bear upon the practical arts it is *not* usually by the procedure of the hypothesis, the experiment, and the theory, but by the empirical method of direct experimentation. It must warm the heart of the applied biologist to quote John Hunter's famous advice to Jenner: 'Don't think; try the experiment!' For to try experiments without too much thought is often the quickest way of arriving at a practical objective. When the limits attainable by such experimentation have been reached, scientific study of the problem may lead to a new outlook and provide the starting-point for a new empirical attack.

For man is an empirical animal. Each new advance in scientific discovery provides him with new weapons for his irrational procedure. His empiricism often leads to surprising observations which could never have been made if every step in the procedure had been rational. That, of course, is why bad experimenters can sometimes get results where good experimenters fail. Claude Bernard missed the presence of trypsin in the pancreatic juice because he was so skilful as a surgeon that he obtained juice uncontaminated by the contents of the duodenum and so the trypsinogen remained inactive. And how many new discoveries in organic chemistry have been made because the operator broke the thermometer?

The production of a new material or a new process is soon followed by its trial for all kinds of purposes, a series of 'experiments' the results of which may provide the basis for subsequent systematic investigation and rationalization by scientific research. We are impatient, and such random experiments are often the quickest way of getting results. A large part of scientific research consists in proving what we have already learned by such methods; scientific research is a slow way of gathering information, but information so obtained is more likely to survive.

In 1939 P. Müller and his colleagues discovered the insecticidal properties of the chemical now known as DDT. In 1944, Läuger, Martin and Müller wrote up a fascinating account of the steps which led to the discovery. I do not pretend to know whether these were the logical steps which were actually followed or whether (as in the writings of most of us) the logic was inserted afterwards to give coherence to the story. What is quite certain is that few would now accept the toxicological basis of their argument, which turns on the hypothetical association of particular chemical groupings with particular types of toxicity. In the parallel case of the discovery of the gamma isomer of benzene hexachloride, there has never been any suggestion that this was a product of the human reason; it was discovered by the wholly empirical procedure of testing as potential insecticides any chemical that chanced to come to hand.

What immediately caught the eye was that both these chemicals were heavily chlorinated aromatic compounds. The significance of this has not yet been adequately explained, but it led chemists all over the world to set about chlorinating every ring compound they could think of; with the result that we now have upon the market a further series of potent synthetic insecticides. Some day scientific research will have to provide an understanding of these triumphs of empiricism.

We have had an instructive example of the relation between scientific research and applied biology in the problem of the fruit tree Red Spider Mite, which has been engaging the attention of orchardists increasingly in recent years. Ten years ago it was agreed as between the Agricultural Research Council, The Pettar Society of Insecticide Manufacturers and the Ace Growers to undertake a joint attack upon this problem. The investigation was planned upon a broad front. Direct trials of insecticides were made against the mite and its eggs; the life cycle and habits of the mite were studied in the field; its relation in competition with the rest of the fauna of the orchards was studied. In the laboratory, the behaviour of the mite, and the nature and determination of the diapause in the overwintering egg were studied in great detail; and finally the complex nature of the egg shell and its relation to the entry of insecticides were partially unravelled.

As the result of ten years' study we have now for the first time a real understanding of the life of this mite. No one working on this problem in the future can fail to benefit from all this knowledge (incomplete though it is) which enables one to think intelligently about this pest in a way which was quite impossible in the past, and to utilize to some extent the natural fauna of the orchard as a contributory factor in control. From the practical standpoint the investigation was wholly successful, for new methods of control have been introduced into the orchards which appear to have solved the problem. But the interesting point is this: control is being effected primarily by the use of summer ovicides. The production of these ovicides was based, of course, upon a century of organic chemistry; but from the standpoint of biology this discovery was wholly empirical; it owed nothing to the scientific investigations of the remainder of the team, and their mode of action is unknown!

SCIENCE AS THE BACKGROUND OF THOUGHT

That is not an experience which should in any way discourage the student of the ecology or physiology of insects. Some years ago I had the privilege of attending a luncheon in Winnipeg at which I was asked to speak about the 'contribution of insect physiology to medical entomology'. The burden of my address was that it made no contribution; that is, no *direct* contribution, and it is not its function that it should.

I think that is a matter about which we should be clear. We often hear the young man sigh deeply and say: 'It must have been wonderful when you were starting research and all the field was wide open. Nowadays it is different—everything easy has been done!' And yet we all know that you have only to take up the most familiar matter in pure or applied biology and almost at once you find that almost nothing is known about it. Indeed, most of us thank God for our ignorance, and happily contrast our lot with that of the classical scholar who has long since worked out his mine and is now reduced to picking over the slag heaps in the hope that he may have missed a little of the ore.

The prime contribution of pure science is to make good this deficiency in knowledge. Very rarely can the applied biologist put his finger on some discovery in pure science and say that it was this which solved his problem—but in thinking about any practical problem he is continually making use of the whole range of scientific knowledge that exists about all its component parts.

When one reads the discourteous remarks that are made in certain quarters about 'reactionary mendelismus-morganismus' one might imagine that the professional breeders of plants and animals in Western Europe and the Americas were all geneticists. Nothing, of course, could be farther from the truth. Most of the complex systems with which the breeder is concerned are still beyond the grasp of the geneticist—or he is only just beginning to extend his science to include them. Breeding is an empirical art which relies on gifts of intuition and experience. Even the production of hybrid corn, which is often claimed as one of the practical triumphs of genetics, although based upon a most penetrating genetical analysis, could be fairly described as the result of an informed empiricism operating on a grand scale. The production of the mule, that other classic example of hybrid vigour, certainly owed nothing to Mendel.

No! The role of the geneticist has consisted largely in explaining what the animal or plant breeder has already done. By so doing he gives stability to knowledge, provides starting-points for further empirical steps, and, what is perhaps of equal importance, he provides the background or climate of thought.

I made my approach to the physiology of reproduction and inheritance by the historical method. My early researches were conducted in an ancient volume of Buffon's *Natural History* which I discovered in the lumber room; and I waded through the controversy on whether the female contributes anything to the embryo at conception. Then a year or two later I came across a translation of Haeckel and learned all about the amazing story of the ovum and the spermatozoon. Finally, this must have been about forty years ago, I noticed a slim little volume in the school library entitled *Mendelism*; and being curious to know what on earth mendelism might be I took it down and read all about the particulate inheritance of characters. I am afraid that my knowledge of the subject has not greatly advanced since those days. But what an astonishing range of ideas one is left with: the independent inheritance of characters; recessive characters uninfluenced in heredity by the dominant characters in the zygote; the equal contribution of the sexes; the reappearance of characters in later generations by recombination, and so on and so forth. My point is that even genetics at its simplest provides an indispensable background for thought for the breeder of plants and animals, which he will inevitably have in mind, even when he uses such more or less empirical procedures as progeny selection or hybridization.

There is, indeed, no hard and fast line between what I am calling empiricism or direct experiment and what I am calling scientific research. Both are supported by the same implicit faith in the constancy of natural laws—a faith so absolute that few other religious faiths can equal it. The spread of this faith among people of every kind is perhaps the greatest of all the contributions of pure science to applied biology. It is certainly one of the major contributions of science to farming.

I am far from supposing that such convictions are universal; there is still a widespread belief in magic—which often masquerades as a belief in Science. If we were to take a free vote in the country I think there is little doubt that we should find a majority in favour of the spontaneous generation of complex organisms, a phenomenon which most biologists would class with the miraculous. Nor am I suggesting for a moment that the farmer should be made to 'think scientifically'; that is, 'to adopt the mental process necessary for the satisfactory pursuit of experimental science: to demand severe standards of evidence and proof, to draw no conclusion that is not strictly justified by the evidence, to leave in suspense any decision for which the materials are not quite complete'. The last thing the farmer can afford to do is to exercise scientific suspense of judgement. To advise him to think scientifically would risk paralysing his judgement rather than activating it. No! The practice of agriculture, like the practice of medicine, or of Government, is a practical art which demands not the limited instrument of the scientific method but a soundly cultivated judgement. And one element in the cultivation of that judgement I hold to be a sympathetic familiarity with the outlook and achievements of science, pure and applied. That is all the more necessary to-day, when, as part of his improved technique, the charlatan adopts the language of science (that itself is indeed a highly lucrative form of applied science) and it is no easy matter to distinguish the genuine from the spurious.

PURE SCIENCE AND APPLIED BIOLOGY IN THE FUTURE

Thus far we have been thinking mostly of the past. What of the present and future? During the later years of the last war the Royal Society set up a number of committees to advise upon the post-war developments of science. It is encouraging to glance at the report of the Biology Committee and to see how many of the recommendations, such as the extended teaching of genetics in the universities, the establishment of centres of research in terrestial ecology, the encouragement of the study of microbiology, and others, either have been or are being implemented. One problem which came before that Committee was how to provide financial support for projects of research in pure science which did not fall within the province of any of the official Research Councils. I remember putting forward the proposal that each of the three Research Councils should set aside a proportion of their block grant to be used in the support of desirable research projects in pure science which did not clearly come within the spheres of interest of any one of them alone; these grants to be allocated by a joint committee of the three bodies. Ultimately I found myself (probably quite rightly) in a minority of one in support of this proposal; it was considered more desirable that the Department of Scientific and Industrial Research, the Medical Research Council and the Agricultural Research Council should each look after the fields of basic research on which they felt themselves to be most dependent in their respective spheres.

Thus the D.S.I.R., for example, makes grants for any research proposals which are of exceptional 'timeliness and promise'. The difficulty is that the most original ideas are at the outset both unpromising and untimely. Only research which is totally unfettered can advance into the most unpromising fields. Writing of conditions in the United States, Prof. Paul Weiss has pointed out that the system of allocating funds for a specific purpose is admirably suited for development work: when the main framework of knowledge exists and we merely want to fill in details or extend the work along some obvious lines. It is likewise suited for organizing trials of some existing theory, collecting more extensive data, or elaborating some existing technique. It is not suited for encouraging the most original research. Weiss has therefore recently proposed that 'all foundations, organizations and individuals who contribute financially to the advancement of medicine, assign a fixed fraction of their budgets, perhaps no more than 10%, to a common pool for the promotion of the biological sciences as such, with no earmarks, no qualifications and no restrictions other than those of accepted accounting procedure. This pooled fund ought to constitute the risk captial of the biological sciences, to be used...as a mobile reserve for the support and encouragement of men with ideas.'

Whether or not there is any solution along these lines, the problem certainly exists and will probably grow in importance. As university salaries and other overheads increase, a relatively greater proportion of the total funds available are deflected away from the costs of research. As a result, the universities become ever more dependent upon outside aid and, apart from direct support by industry, that means support by the three Research Councils. This puts greatly increased power, in the determination of the direction of research, into the hands of the Research Councils—all of which have practical objectives.

If that power were exploited to the full it could, in the short run, produce a great output of applied science; but, in the long run, as everyone concerned realizes, it could lead to the drying up of the sources of new ideas in fundamental science. For it is almost impossible to expect the Research Councils to support original fundamental work in scientific research. Given knowledge, sympathy and imagination they can encourage branches of scientific study that lie at the base of the practical arts in which they are interested. They can support studies on enzymes, vitamins, and antibiotics, or growth hormones in plants, or they can establish research units in plant nutrition, soil bacteriology or insect physiology—because we already know about the importance of such things. But I very much doubt whether it would have been reasonable for the A.R.C. to have supported, for example, Darwin's experiments on the curving of bean shoots or the early experiments of the Wents on the growth of the oat coleoptile—because no one could have foreseen the impact that these observations were going to have on the agriculture of the future.

But at least the Research Councils should take great care not to impede the advance of pure science. We sometimes hear complaints that the universities are not interested in the needs of the applied sciences. I hope I have said enough to make clear my conviction that some contact with the requirements of industry (including of course agriculture and medicine in that term) can be extremely stimulating to the research worker in pure science. But it would be most dangerous to go further than that. Knowledge is a delicate plant, and this audience above all will not need to be reminded that it is an undesirable practice to keep pulling plants up to see how the roots are getting on. We know too that the farmer does not grow plants—it is the plant which grows, the farmer merely provides it with a favourable environment for the process.

We must therefore have a wide margin of enthusiasts in the universities whose inquiries are *totally* unrestricted. It will be an unhappy day when the Research Councils use their growing powers to invade this field. It is notoriously difficult to foresee just which discoveries in pure science will prove to be of practical value.

When writing the first edition of his *Grammar of Science* in 1892, Karl Pearson gave as an example of a discovery which had no apparent practical value, the recently described Hertzian waves, now the waves of radio (though, with prophetic caution, he added that that man would be a bold dogmatist who would venture to assert that this discovery could not, in a generation or two, do more to revolutionize our lives than the frog's legs of Galvani). Who could possibly have foreseen where the infant organic chemistry of 120 years ago was going to lead—for at that time it had no conceivable connexion with industry? Who can foresee to-day where theoretical chemistry is going to lead? Is it possible that this may provide the real key to the biology, medicine and agriculture of the future? Yet no one could reasonably expect the Agricultural Research Council to finance projects in theoretical chemistry on that account.

In short, the opinion on the relation between pure science and applied biology which I have been trying to express is one that is highly equivocal. Pure science provides the new tools that can be used by the applied biologist. When and where these new tools are going to be produced is utterly unpredictable and is not amenable to planning. Therefore the applied biologist should refrain from disturbing the pure scientist in his studies. On the other hand, to disturb him, to wake him up, and bring to his notice some of the unexplained phenomena that are met with in agricultural or medical practice may be just the way to stimulate his interest and his intellect and to cause him to open up some vast new field of knowledge.

We are perhaps inclined to think too often of these new tools of which I have just spoken as things like antibiotics, or vitamins, or new groups of insecticides, or synthetic plant hormones. But these are only valuable side products of pure science. The primary objective of science is to provide the theories which are the tools of thought. It is to equip the mind with *these* tools that we insist that the applied biologist should have a thorough grounding in pure science. *That*, I submit, is the real contribution of pure science to applied biology.

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RESEARCH TRENDS IN CANADIAN AGRICULTURE AND FORESTRY

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INTRODUCTION

The range of climatic conditions under which agriculture and forestry are practised in Canada is such that enterprises and problems associated with them are enormously varied. Agriculture varies from peaches and tobacco in southern Ontario, where the average frost-free period is over 150 days, to early-maturing cereals, hardy vegetables and bush fruits in northern Alberta, where only 75 or fewer frost-free days can be expected. In areas of commercial forest, annual precipitation varies from less than 20 to more than 200 inches. Geologic and climatic differences are reflected in a wide range of soil conditions, and various combinations of climate, soil and vegetation, natural and cultivated, are inevitably associated with a varying multitude of weeds, diseases and destructive insects that are as fascinating to the biologist as they are disturbing to the farmer or forester. Many of our problems arise from our own activities and, since experience has been relatively brief, it is not surprising that the emergence of new and unexpected complications is frequent. Despite our somewhat inhospitable climate, a wide variety of introduced pests find conditions in Canada more congenial than those prevailing in native habitats. These and other conditions are undoubtedly important in relation to the unpredictability of the relative importance of various problems.

Biological instability is characteristic of our farms and forests. Many species of destructive insects habitually vary in a given region from marked scarcity to plague proportions. For example, before the present spruce budworm outbreak in New Brunswick, this insect failed to appear for several successive years in forest insect survey collections. The forest tent caterpillar, the hemlock looper, the armyworm, some species of grasshoppers, and many other insects behave similarly. Wireworms, the wheat stem sawfly, the codling moth, the larch sawfly, and bark beetles, to name but a few, fluctuate much less violently. Likewise, many plant diseases flourish periodically though the conditions regulating their abundance are probably less complex than with insects.

I do not pretend that the conditions I have described are peculiar to Canada, or to North America, but they are very pronounced and they contribute materially to the difficulties, and also the interests, of applied biology. For example, investigations on the control of insects or diseases, whether they be concerned with cultural practices, chemicals or host resistance, can proceed apace if outbreaks or epidemics can be purposely established in field experiments; but if, as is often the case, the investigator must await natural occurrences, progress may be very slow.

The number and complexity of economic problems, sparse population and, consequently, limited research resources have, at least until very recently, interfered seriously with the proper organization of research programmes. Moreover, we have enjoyed an abundance of fertile agricultural land and productive forest, and even now the Canadian public shows little sign of awareness of the limitations of our resources and much less of the significance of biological research in relation to their maintenance or renewal.

ORGANIZATION AND HISTORICAL DEVELOPMENT

Organized agricultural research in Canada began with the establishment of the Central Experimental Farm in Ottawa in 1886, and others about the same time at Agassiz, B.C.; Indian Head, Sask.; Brandon, Man.; and Nappan, N.S. From this beginning, until the end of the First Great War, the research of the Canada Department of Agriculture, which, until 1909, was all conducted by the Experimental Farms Branch, was mainly concerned with field studies on soils, crops and livestock and the essential preliminary steps in plant protection, namely, the identification of insects, diseases and weeds, studies of host ranges and geographic distribution, life-history studies and control measures. Plant breeding, notably of cereals and fruits, has from the beginning been prominent in the work of the Central Experimental Farm.

Shortly after the turn of the century, several additional experimental stations were established. At present, besides the Central Experimental Farm and various laboratories at Ottawa, there are thirty experimental farms and stations, fifteen experimental substations, two forest nursery stations and fourteen laboratories.

In 1909, entomology was detached from the Experimental Farms Branch and established as a separate branch of the Department. In 1938, the Department was reorganized. The intention, so far as I can ascertain, was to assign work in the various 'husbandries' to Experimental Farms Service and to concentrate research in Science Service. At first, Science Service was composed of four divisions: namely, Entomology, Botany and Plant Pathology, Chemistry, and Bacteriology. Later, the Division of Animal Pathology was transferred to Science Service and, also, the Division of Plant Protection. In 1952, the Division of Animal Pathology was transferred to Production Service in order to provide more intimate working relations with the Health of Animals Division. The distinction between Experimental Farms Service and Science Service is manifestly artificial, particularly since plant breeding is a function of the former; but working relations are such that the administrative cleavage is not a serious impediment.

I have said that until the end of the First Great War the research divisions of the Department of Agriculture were devoted mainly to work of an essentially practical nature that inevitably dominates agricultural research in a pioneer country. However, during this period a highly significant, if modest, amount of research in botany and zoology was in progress in several Canadian universities. Also, botanical studies were an important feature of the geological survey of Canada. Notwithstanding the danger attached to generalizations without evidence, I think it is safe to say that, until the early or middle 'twenties, agricultural research was of a decidedly practical nature in the Canada Department of Agriculture and largely academic in our universities. Probably an essential qualification is that related to the applied research carried on for more than half a century at the two French-speaking agricultural colleges in the Province of Quebec, at the Ontario Agricultural College, and, more recently, at others.

The National Research Council, founded in 1916, has had a profound influence on scientific research in Canada, including that related to agriculture. The researches of the Division of Biology and Agriculture, now the Division of Applied Biology, important and valuable as they are, are overshadowed by the benefits derived by all agricultural research agencies from post-graduate scholarships and financial support of research in Canadian universities. These two enterprises, combined with the establishment of various associate committees that have served to facilitate critical reviews of regional and national research programmes, have conferred enormous benefits that have become increasingly apparent since the late 'twenties. Among the discernible effects are more intimate relations between university and government laboratories, and improved standards of staff selection and training with attendant benefits to university and government laboratories alike. There is no doubt that government research in agriculture and forestry is more scientific than it was 20, or even 10, years ago and I am inclined to think that universities are now more active in applied research, and I hope they are not, as a result, becoming less academic.

It is impossible, and for my present purpose unnecessary, to attempt a complete description of the organization of agricultural research in Canada. Notwithstanding significant activity by some provincial government agencies, notably the Ontario Department of Agriculture, agricultural research is dominated by the Canada Department of Agriculture and agricultural faculties of the universities. In certain fields, especially entomology and plant pathology, the Canada Department of Agriculture is, allowing for a few exceptions, the sole research agency. This, in my opinion, can be counted as one of our weaknesses. An expansion of university research in these fields would enhance the value of the national programme not only by work done but also, and this is perhaps more important, by improving the standard of undergraduate and post-graduate instruction.

Unlike farms, Canadian forests have offered abundant ready-made harvests and this fact has undoubtedly influenced the course of research. The Forestry Branch of the Department of Northern Affairs and National Resources maintains five forest experiment stations for silvicultural research and also conducts experiments on provincially and privately owned land. Forest fire research is conducted at several widely separated stations.

The genetics and breeding of forest trees is a field that has suffered serious neglect. Useful work, on a very limited scale, is being done by the Forestry Branch at the Petawawa Forest Experiment Station in Ontario and by the Ontario Department of Lands and Forests at Maple.

The Forestry Branch maintains two well-equipped laboratories for forest products research, at Ottawa and at Vancouver, B.C.

Research on forest insects was one of the major functions of the Division of Entomology of the Canada Department of Agriculture almost from the beginning. In 1951, forest entomology and forest pathology were detached from the divisions of Entomology and Botany and Plant Pathology, respectively, and combined to form the Forest Biology Division. As the Systematic Entomology Unit and the Biological Control Unit of the Entomology Division also serve the forest entomologists and the Entomology Division engages in some non-agricultural studies, it is probable that forest entomology, as such, commands resources almost equal to those provided for agricultural entomology.

Forest Pathology received very little attention until 1946. There are now over thirty research officers in seven laboratories of the Forest Biology Division and at least two university professors investigating forest tree diseases. The main responsibility for taxonomic studies on fungi that cause tree diseases rests with the Botany and Plant Pathology Division.

There are forestry faculties in four Canadian universities. They have displayed very little research activity. This unfortunate state of affairs can probably be attributed to the fact that university training has been aimed very largely at meeting the immediate professional needs of the industry. The nature of these needs must inevitably change as the supply of readily accessible mature timber diminishes, and we may expect that the universities will respond with changes in emphasis that to be effective must be accompanied by research.

By way of illustrating some of the foregoing generalizations, I have prepared reviews of three very different research undertakings. A measure of judgement was exercised in the selection of these topics, but they were not deliberately selected so as to cast an unduly favourable light on Canadian research in agriculture and forestry!

Ecological studies on apple orchard fauna

In view of the very wide range of climatic conditions under which apples are grown in Canada, it is only to be expected that a complex variety of disease and insect problems should confront the growers. Variations in conditions are such that it has been necessary to undertake investigations on pest control at seven research laboratories distributed from Nova Scotia to British Columbia. The necessity for devising, as quickly as possible, reasonably effective and economical controls, and the inescapable burden of testing new fungicides, insecticides and acaricides, have seriously limited the resources available for critical long-term biological studies. Enough has been done, however, particularly during the last twelve years, to show clearly that the scientific and economic rewards are ample to justify expanded and intensified biological research. The pattern of work designed at the Fruit Insect Section, Science Service Laboratory, Kentville, N.S., together with results already obtained, serve to define a course that should be followed diligently for a long time to come.

According to Pickett, Patterson, Stultz & Lord (1946): 'During the early part of this century, fruit of good quality was produced with 2 or 3 applications of spray applied with hand-operated pumps. To-day, with greatly improved equipment and spray chemicals, 6 to 10 applications are required to produce crops reasonably free of insect damage.'

During the past 12 years, studies at Kentville have been directed mainly at the effects of various spray programmes on orchard fauna. The aim has been to include consideration of all important species of destructive insects and mites and of parasitic and predacious species that attack them. Experiments have been carried out in neglected orchards in which the fauna had not been subjected to the influence of sprays for several years and, also, in commercial orchards in which various spray programmes were followed. One study on the influence of climatic factors, particularly minimum temperatures, has been completed.

In Nova Scotia, there is no alternative to the use of fungicides for controlling apple scab, *Venturia inaequalis* (Cke.) Wint. Since observations indicated that fungicides in common use had a pronounced effect on the abundance of some important pests, this problem has been given special attention.

Investigations on the oystershell scale and the European red mite have yielded particularly significant results and, excepting a few general remarks, this review is confined to them.

Oystershell scale, Lepidosaphes ulmi (*L.*)

The history of the oystershell scale in Nova Scotia has been reviewed by Lord (1947), and it need only be stated here that since 1930 it has become a very serious pest of apples.

In 1943, experiments were begun to determine the influence of fungicides on the scale and its two most important natural enemies, the predacious mite *Hemisarcoptes malus* (Shimer), and the parasite *Aphytis mytilaspidis* (LeB.).

Two typical examples of results obtained are provided by the data in Table 1. These data were selected by Lord from tables 2 and 4 in his paper to which reference has already been made. Both orchards were sprayed as required to control apple scab. Extensive and detailed studies of populations of *A. mytilaspidis* and of *Hemisarcoptes malus*, made in various experimental orchards, have demonstrated clearly that these two species will control the oystershell scale in Nova Scotia apple orchards if they are not suppressed by ill-advised spray programmes. The use of mild sulphurs for controlling apple scab interferes with parasitism and predation to such an extent that the scale is likely to cause very serious damage. Lime-sulphur is toxic to the scale as well as to its natural enemies, but because of phytotoxic effects its use is not recommended. Neither fermate nor copper sprays interfere with the activities of *Aphytis mytilaspidis* and *Hemisarcoptes malus* and the control of the scale indicated in Table 1 is attributed to them.

TABLE 1. *Effects of fungicides on the natural control of the oystershell scale on apple trees as shown by changes in the scale population*

Material	Oystershell scales per 100 terminals				
	1943*	1944	1945	1946	1947
Palmer Orchard					
Fermate	264	562	3	6	—
Lime-sulphur	554	233	36	138	—
Flotation sulphur	692	550	633	1036	—
Hiltz South Yarmouth Orchard					
Bordeaux and C.O.C.S.	—	—	2	3	6
Flotation sulphur	—	—	72	338	458

* Initial population

European red mite, Metatetranychus ulmi (*Koch*)

Since most, if not all, fungicides and insecticides are more or less selective in their effects on the various species of arthropods inhabiting orchards, it cannot be expected that a spray programme that encourages the natural enemies of one pest species will be useful in connexion with another. Indeed, the complexity of apple orchard fauna is such that any change in spray practices is almost certain to be reflected in changes in the relative abundance of various species of arthropods. It follows that so long as we continue to employ new chemicals we can confidently expect new problems.

The European red mite provides a striking example of a species capable of responding very quickly to spray practices that discourage its natural enemies. The investigations of Lord (1949) have revealed over thirty species that prey upon the European red mite. The two most important of these were the mite *Iphidulus tiliae* (Oud.) and the thrips *Haplothrips faurei* Hood. Much of the work consisted of very extensive quantitative studies of populations of the red mite and its predators as affected by fungicidal spray chemicals, particularly copper compounds, mild sulphurs and fermate.

Results of these experiments indicate clearly that sulphur is highly toxic to *Iphidulus tiliae* and *Haplothrips faurei* and that the red mite multiplies very rapidly in orchards where sulphur is depended upon for controlling apple scab. Fermate is detrimental to *Iphidulus tiliae* but appears to be innocuous to *Haplothrips faurei*; yet the latter species is often not sufficiently numerous to suppress the red mite in the absence of *Iphidulus tiliae*. Normally, a complex of predators, including this thrips, reduces the likelihood of red mites reaching as high a level under fermate as under sulphur spray. According to the author, 'In the few instances in which all-copper fungicides have been used in commercial orchards and experimental plots, the red mite has become of minor importance after the first year, and has thereafter remained consistently low as a result of effective predation by its natural enemies.'

The red mite problem in Nova Scotia is not, of course, due solely to the effects of fungicides. Insecticides may be equally or more significant. At present, the codling moth, *Carpocapsa pomonella* (L.), is the most serious insect pest of apples in Nova Scotia. Much work has been done, and important results obtained, on orchard spray programmes as factors in the ecology of the codling moth. Preliminary studies undertaken in 1953 on ryania in comparison with DDT for codling moth control included periodical records of the red mite and of predacious mites. The results have been published by Pickett & Patterson (1953) and the data in Table 2 are derived from their paper. Pronounced differential effects of the ryania compounds and DDT on the red mite and on predacious mites are evident as, also, is the practical significance. Other experiments showed that ryania compounds are not toxic to the red mite.

TABLE 2. *Comparison of effects of DDT and two ryania compounds on the European red mite and predacious mites in apple orchard plots* 1953

	Mites per hundred leaves		
	DDT	Ryanexcel	Ryanicide
	European red mite		
25 June	35	20	5
9 July	65	130	170
22 July	155	125	45
6 August	695	75	25
28 August	2030	50	25
	Predacious mites		
25 June	20	10	25
9 July	10	40	40
22 July	0	70	45
6 August	0	125	120
28 August	0	35	50

The biotic factors important in fluctuations of populations of the European red mite appear to be more complicated than those for the oystershell scale. Nevertheless, it is clear that efforts to control this mite are likely to fail unless careful consideration is given to unintended effects. Although many shadows remain, much light has been shed on a very complex faunal society.

Cold tolerance of Aphytis mytilaspidis

As an initial step in extending ecological studies to include climatic factors, Lord & MacPhee (1953) investigated the minimum temperature under which *A. mytilaspidis* and *Lepidosaphes ulmi* would survive. A preliminary survey in New Brunswick suggested that the abundance of *Aphytis mytilaspidis* might be limited in the central part of the province by the comparatively low winter temperatures prevailing there. Through the co-operation of laboratories elsewhere in Eastern Canada extensive data on parasitism of the oystershell scale by *A. mytilaspidis* and on mortality of the larvae of the parasite were assembled. The data in Table 3 are derived from table 2 in the paper by Lord & MacPhee. A very close positive relation between larval mortality and minimum temperature is apparent.

TABLE 3. *Temperature minima and winter mortalities of larvae of* A. mytilaspidis *in eight localities*

(Data averages of 1949–50 and 1950–1.)

Locality	Minimum temperature (° F.)	Larval mortality (%)
Annapolis Royal, N.S.	−6	13
Simcoe, Ont.	−12	12
Middleton, N.S.	−14	28
Saint John, N.B.	−16	53
Belleville, Ont.	−19	68
Moncton, N.B.	−20	66
Sussex, N.B.	−24	92
Kemptville, Ont.	−27	99

Under controlled conditions in the laboratory, *A. mytilaspidis* larvae and their hosts, *Lepidosaphes ulmi*, were exposed for varying periods to temperatures ranging from −10 to −26° F. In a word, the results of field studies were confirmed. Quoting from the authors, 'Almost 100% of the *Aphytis mytilaspidis* larvae were dead about half an hour after cooling to −20° F. The time of exposure to produce a high mortality increased as the temperature was raised until at −12° F., eight hours' exposure did not give complete mortality. Oystershell scale eggs were much more resistant to cold than the parasite larvae. At −26° to −22° F., three hours were required to destroy 90% of the eggs and at −18° F. about eight hours would be required.'

WHEAT: GENETICS AND BREEDING

Breeding

The problem of stem rust of wheat, caused by *Puccinia graminis tritici* Erikss. and Henn., in the Prairie Provinces, was responsible for the first deliberately planned, comprehensive research programme in agriculture or forestry in Canada. The original plans were made by the National Research Council, the Dominion Department of Agriculture, and the universities of Manitoba, Saskatchewan and Alberta. The Dominion Rust Research Laboratory was established in 1925 and, about the same time, expansion of researches on wheat in the three universities of the Prairie Provinces was facilitated by the National Research Council. The nature and scope of the work to be done had already been clearly defined by earlier investigations by workers at the University of Minnesota, by W. P. Thompson and W. P. Fraser at the University of Saskatchewan, and by A. H. R. Buller at the University of Manitoba.

It is obviously futile to breed wheat for resistance to stem rust without at the same time giving due consideration to all other characters of economic significance in the region concerned. Among important characters, in addition to stem rust and yield, that have been prominent are resistance to leaf rust (*Puccinia triticina* Erikss.), smuts (*Tilletia caries* (DC.) Tul., *T. foetida* (Wallr.) Liro and *Ustilago tritici* (Pers.) Rostr.), rootrots and the wheat stem sawfly (*Cephus cinctus* Nort.); and milling and baking quality. Fortunately, stem rust is a comparatively minor hazard in areas where the wheat stem sawfly is abundant and the sawfly seldom causes widespread serious damage in the rust area. Sawfly research is concentrated mainly at Lethbridge, Alberta, and the rust investigations at Winnipeg, Manitoba. Through an efficient committee organization, plant pathologists, geneticists, cytologists, and cereal chemists, in universities and government departments, have worked in close co-operation for thirty years, and there has been a continual exchange of ideas and materials with United States workers at the University of Minnesota and elsewhere.

On the economic side, the work has been conspicuously successful. From the late 'thirties until 1952, stem rust caused no appreciable damage to hard red spring wheat in Canada. However, all the new resistant varieties that were available in quantity until 1953 are susceptible to the now widely prevalent race 15 B. The new Canadian variety, Selkirk, is resistant to 15 B, but susceptible to a race that appeared for the first time in 1952 and that has not yet become widespread. At this point, it is appropriate to emphasize the importance of the physiologic race survey because, without it, plant breeders would have no warning of new threats. The United States and Canadian surveys extend from Mexico to Canada and international co-operation is such that we are informed as to the racial composition of *P. graminis tritici* in South America, Africa and Australia. Race 15 B was discovered by E. C. Stakman and his associates in 1939, and it was immediately given consideration in breeding plans. Selkirk, as I have said, is resistant to it. Resistance to the new race to which Selkirk is susceptible has been found in a variety obtained from Kenya. According to Dr R. F. Peterson (private communication), results of preliminary tests in Canadian, United States and Latin American laboratories indicate that it is resistant to all races occurring in the Western Hemisphere. This variety, designated Kenya 338.AC.2.E.2, is being employed at the Laboratory of Cereal Breeding, Winnipeg, Manitoba, as the main source of stem rust resistance.

Encouraging progress has also been made in the development of commercially acceptable varieties of wheat that are resistant to the wheat stem sawfly. The variety Rescue was first distributed in 1946 and it rapidly became the most popular variety in areas subject to severe losses from sawfly damage. Rescue is now being largely replaced by Chinook, which is superior in straw strength and commercial quality. An account of the work that led to the production of Rescue has been published by Platt & Farstad (1952).

Possibilities of reducing the time that elapses between hybridization and the multiplication of a new variety, and of increasing the precision of selection in early generations, are being investigated.

For many years, plants of the first hybrid generation have been grown during the winter in greenhouses, and promising selections made in later generations have been multiplied in California. Recently the Cereal Division at Ottawa has succeeded in maturing three generations of spring wheat hybrid material from September to April in a growth chamber provided with appropriate light and temperature controls. Thus if the first generation of a cross is grown in the field one summer, the fifth generation can be sown in the field the following summer. Or, since many undesirable types can be eliminated by selection from F_2 populations in the field, it may be more efficient to use the growth chamber for the third, fourth and fifth generations. If the first crop in the growth chamber consists of 1000 F_3 plants, three seeds of each are planted and one allowed to mature, giving 1000 F_4 plants, and the third winter crop will consist of 1000 F_5 plants. A growth chamber that will accommodate at least 10,000 plants is to be constructed at Winnipeg.

In Canadian spring wheats, baking quality is second in importance to no other character. Its inheritance is certainly not simple and it is profoundly influenced by environmental factors. Conventional experimental baking methods require a minimum of 400 g. of each flour, a circumstance that imposes severe restrictions on the number of lines tested. If it were possible to practise selection in early generations, the average quality of strains subjected to final yield and quality tests could be improved and, hence, the chance of success enhanced. With these considerations in mind, Miller, Edgar & Whiteside (1954) have designed an apparatus for measuring the expansion of fermenting dough balls in weak salt solutions. Only 20 g. of flour are required for each strain to be tested. Experimental studies on the relation between results of the expansion test and loaf volume determined by conventional baking methods revealed a very close positive relation between the two variables. In two series, one consisting of 107 strains and the other of 80 strains, correlation coefficients were 0·80 and 0·90 respectively. A micro-mill, an obviously essential tool, is being designed and constructed by the Cereal Breeding Laboratory, Winnipeg, Manitoba. This mill is expected to produce flour from 25 g. of wheat.

Genetics

Researches on the genetics and cytology of wheat are in progress at laboratories of the Canada Department of Agriculture in Ottawa, Winnipeg and Lethbridge, and at the universities of Manitoba, Saskatchewan and Alberta. At least a dozen well-qualified geneticists are devoting all or most of their time to the genetics and cytology of species of *Triticum* and related genera. Historically, this development has taken place largely under the influence of W. P. Thompson, as teacher and investigator, supported, of course, by the overriding importance of wheat on the Canadian prairies and the losses attributable to cereal rusts and smuts and the wheat stem sawfly. In an interesting review, Thompson (1949) discusses the significance of cytogenetic researches in relation to wheat improvement and includes a concise account of his own work on inter-specific and inter-generic crosses.

Although there is still much to be learned about the genetics of *T. aestivum*, and work continues, particularly in relation to reactions to rusts, smuts and sawfly, the possibility of effecting improvement by introducing characters from other species and genera is being investigated. Particular interest is being displayed in the method of nullisomic analysis, developed by Sears (1953), which, besides facilitating increased refinements in the genetic analysis of common wheat, provides a means for substituting one or more entire chromosomes derived from other varieties or related species. The method has been employed by Larson (1952) in her studies of the inheritance of stem solidness, a character associated with resistance to the sawfly. She concludes that 'Chinese spring and S-615 differ by at least four genes for solidness', and she has identified the chromosomes on which these genes are located.

Unrau (1950) has employed the same method in his studies on chaff colour, spike density, awning and other characters. In a private communication, Dr B. C. Jenkins has outlined a method being employed at the University of Saskatchewan in the hope of increasing the hardiness of winter wheat. An aneuploid series is being set up in Kharkov M.C. 22 winter wheat. An 'addition' series consisting of seven types each with the full complement of Kharkov chromosomes plus one of the chromosomes derived from Dakold winter rye is being established. The final step will involve crosses between the deficient and the addition lines. Theoretically, it will be possible to produce 147 different winter wheats each with 20 pairs of chromosomes derived from Kharkov wheat and one pair from Dakold rye.

Because the capacity of parasitic fungi to vary appears to be little, if at all, less than that of their hosts, genetical studies in the genera *Puccinia*, *Tilletia*, *Ustilago* and *Fusarium* have been well represented in the Canadian wheat research programme.

Limitations of space forbid more than passing reference to the work in plant pathology and cereal chemistry. In both fields, the scientific achievements alone more than justify the effort. At present, in co-operation with plant physiologists and chemists, plant pathologists are pressing forward with the almost infinitely complicated problem of host-parasite relations of cereal rusts.

In terminating this section, I cannot do better than quote Dr W. P. Thompson (1949), referring particularly to the production of rust-resistant varieties of wheat:

'The whole enterprise is an excellent example of co-operation in research. It involved the combined efforts of several plant pathologists each working on his own phase of the problem, a group of breeders amongst whom were divided the most promising crosses, agronomists, cytogeneticists, biochemists working on the nature of resistance and cereal chemists working on milling and baking qualities. These investigators were located in several different institutions from Edmonton to Ottawa and in different departments of individual institutions. It is known, of course, who carried out the particular crosses which produced the varieties now used but the happy outcome is the result of the combined efforts of the whole group and all deserve a share of the credit.'

THE SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA* (CLEM.)

Of the many species of destructive insects inhabiting Canadian forests, the spruce budworm is by far the most important. It is a native insect with a range extending from coast to coast. In Eastern Canada it feeds, in order of preference, on balsam fir, *Abies balsamea* (L.) Mill; red and white spruce, *Picea rubens* Sarg. and *P. glauca* (Moensch) Voss; and some other conifers. In British Columbia, the favoured hosts are various species of true fir, *Abies*, Douglas fir, *Pseudotsuga taxifolia* (Poir.) Britton, and spruce. Serious economic damage to species other than balsam fir and white and red spruce is exceptional and even spruce suffers severely, as a rule, only when growing among or near balsam fir. Since the pulp and paper industries in Eastern Canada are largely dependent upon balsam fir and spruce, and because damage caused by the spruce budworm is enormous, the problem is one of first-class importance. Estimates of average annual losses in terms of pulpwood volume, though crude, are probably conservative, and amount to more than half the volume of pulpwood harvested annually. Economically, increased fire hazard and effects on the composition of succeeding stands may, according to de Gryse (1947), be even more important.

Canadian work on the spruce budworm began in 1909, but was confined largely to observation and surveys until 1919, when the studies reported by Swaine, Craighead & Bailey (1924) were begun. Included in these studies were the history of earlier outbreaks by means of ring patterns of surviving trees, life history and feeding habits of the insect, dispersal of larvae and adults, susceptibility of host species and stand types, and significance of associated insects, particularly bark beetles and wood borers. These studies did not include consideration of predators, parasites, or diseases.

From 1924 to 1944 very little work was done. Through the forest insect survey, important data were accumulated on the location, intensity and duration of outbreaks, and on parasitic enemies of the budworm; but there was no comprehensively planned programme of research.

Since 1909 Eastern Canada has not been free from local or regional infestations of the budworm. Damage caused in Ontario and western Quebec between 1935 and 1945 was of such concern to the forest industries that a comprehensive, long-term research programme became imperative. During the war, plans were carefully prepared by J. J. de Gryse and his associates, and, with the co-operation of industry and several provincial governments, an enormous expansion of work began in 1945. In that year, the Province of Ontario erected a modern laboratory at Sault Ste. Marie, Ontario, which was staffed and equipped by the Canada Department of Agriculture. In 1950, also at Sault Ste. Marie, a building specially designed and equipped for fundamental research in insect pathology was completed. Field stations were established in northern and north-western Ontario, in co-operation with the Provincial Government and the industry, for intensive ecological studies of the budworm problem. In the Green River watershed in north-western New Brunswick, a field station was established in 1944 as a co-operative undertaking of the Forest Biology Division, the Dominion Forest Service, the New Brunswick Department of Lands and Mines, and Fraser Companies Ltd., the industrial unit operating the pulpwood forests of that area. At this time, in the Green River watershed, the spruce budworm was just beginning to 'emerge' from its endemic state, and the plan of work called for detailed ecological studies embracing all possible influential factors from the beginning of the outbreak to its termination. Permanent laboratories in Quebec City, Quebec; Truro, N.S.; and others in Western Canada are also active in spruce budworm investigations.

Concise and well-documented reviews of recent work have been written by Prebble & Morris (1951) and Prebble (1954). An attempt is made here only to outline the nature and scope of the research programme and to comment briefly on certain aspects that seem particularly significant or interesting.

History of earlier outbreaks

Reference has already been made to the studies of Swaine *et al.* (1924). A particularly favourable opportunity for detailed investigations was provided in the Lac Seul area of north-western Ontario, where the present outbreak, now involving about 10,000 square miles of territory, began about 12 years ago. Blais (1954), by means of studies of ring suppression patterns of white spruce, traced the development of an outbreak beginning in 1866 and terminating about 1872. The area involved corresponds very closely to that of the present infestation, and the localities of initial infestation and the spread from them were similar in the two periods. It is concluded that all mature balsam fir in the area was destroyed in the earlier outbreak and that the recent, susceptible, mature balsam developed from seedlings established before 1866. There is no evidence of the establishment of balsam seedlings for about 40 years after the end of the earlier outbreak. It was not until comparatively recent times that the forest again became susceptible to attack because, as indicated below, mature or over-mature balsam is the most important element in stand susceptibility.

When this study was undertaken, the area had never been disturbed by cutting. It was virgin forest. This and, no doubt, other factors led Blais to conclude that 'since the forests in this area had never been subjected to exploitation, all changes in the forest composition and all related phenomena are entirely natural. Spruce budworm outbreaks, therefore, appear to be a phase in a natural cycle of events associated with the maturing of balsam fir.'

Methods of sampling

In almost any phase of spruce budworm research it is essential to devise and employ methods of sampling that will not make excessive demands upon staff, yet will describe population intensities, at any stage from egg to pupa, and host defoliation in terms that will provide for reliable comparisons through space and time. In an effort to minimize the likelihood of conflicting results attributable to sampling methods, this matter has been given careful attention. For a brief summary and for references, the reader should consult Prebble (1954).

Stand susceptibility

From a purely practical point of view the objective of researches on the budworm is the management of the forest so as to reduce its vulnerability to budworm attack. It becomes necessary, therefore, to define the characteristics of resistant and susceptible forest types.

The work of Morris (1951) and Blais (1952) indicates clearly that the most significant single characteristic of a susceptible stand is a high incidence of flowering balsam fir. Newly emerged, second-instar larvae are reluctant to feed on old foliage, yet they commonly emerge from their hibernacula before foliar buds of the current season burst. Male flowers, which open before the foliar buds burst, are a favoured source of food which fills the gap between the emergence of larvae and the opening of new foliar buds. Moreover, laboratory experiments have demonstrated that larvae forced to feed on old foliage give rise to smaller pupae and less fecund adults.

Another significant feature of flowering trees is the persistence of the cuplike bracts subtending male flowers. These bracts persist for as long as 25 years. They are particularly favoured by the larvae as sites for hibernation.

Additional considerations of importance are, first, that oviposition is relatively abundant on flowering trees and, secondly, that flowering reduces greatly the production of new foliage. Thus larval populations are concentrated and new foliage is destroyed more rapidly by a population of given size.

In the areas of recent outbreaks in Eastern Canada, there is a wide variation in the proportions of broad-leaved and coniferous types and in the numbers of the various species of each. Of several attempts to define vulnerability in quantitative terms, Turner's (1952) is the most comprehensive. This work was done in an area that had been heavily infested from about 1936 to 1945 and the mortality of balsam fir was determined in various forest cover types. Systems for rating vulnerability designed by other investigators were found to be unreliable. In several plots that would, by other methods, be rated resistant, mortality was high. In general, percentage mortality increased with basal area of fir per acre and height of fir and where the coniferous components of the stands were mainly fir and spruce. However, reliable prediction of mortality in a given area depends upon several other factors, among which may be mentioned the duration of an outbreak, isolation by resistant stands, proximity to focal points of the outbreak and prevailing wind direction.

Mortality of balsam fir in relation to duration of infestation

Aside from its intrinsic interest, this subject is important in relation to planning salvage operations and to timing the application of insecticides. Results of an intensive study by Belyea (1952) extending over the period 1946–1951, in the Lake Nipigon area of Ontario, showed that mortality began in the fifth year of severe defoliation and was complete or nearly so in the eighth year. This study included consideration of the possible effects of attacks by bark beetles and wood borers. Ten species were studied, and it was concluded that in no case was death of the host tree hastened by their activities. Mortality was due entirely to severe and prolonged defoliation.

Salvage of budworm-killed trees

This problem has been investigated by R. M. Belyea and J. T. Basham (unpublished results). Briefly, it was concluded that, for lumber, logs were destroyed by borers about 1 year after death, and that pulpwood was ruined by decay in about 3 years.

Bioclimatology

The work of W. G. Wellington and his associates on the effects of physical factors on the behaviour and development of the budworm and the forest tent caterpillar (*Malacasoma disstria* Hbn.), and on the interrelations of climatic cycles and the epidemiology of these two species, is of conspicuous interest and importance. It is with reluctance that I omit reference to field and laboratory researches on light, temperature and humidity in relation to budworm behaviour. For citations, the interested reader is referred to Prebble (1954).

The relation between the occurrence of budworm outbreaks and the frequency of cyclonic centres in eight regions of Eastern Canada has been studied by Wellington, Fettes, Turner & Belyea (1950). Dates of the initial stages of the outbreaks ranged from 1909 to 1940. The 3- to 4-year periods preceding budworm outbreaks were characterized by negative deviations from the average annual number of cyclonic centres passing over the areas concerned and by reduced precipitation in June and July. The meteorological evidence of drought was supported by a reduction in the radial increment of trees prior to budworm outbreaks.

The authors conclude that budworm outbreaks result from susceptible stands plus climatic release. As a result of this conclusion, they argue that dispersal of the spruce budworm is less significant in relation to epidemiology than had formerly been supposed, and that outbreaks usually originate with endemic populations.

Weather conditions that favour increases in populations of the forest tent caterpillar are in marked contrast to those favouring the spruce budworm. Convincing evidence of the influence of positive deviations from the average annual number of storm centres passing over a region being conducive to forest tent caterpillar outbreaks is presented.

In a more recent paper, Wellington (1952) reports on an extension of the study to include origins of air masses and circulation patterns. He concludes:

> 'The required physical conditions for spruce budworm population increase tend to occur in northern Ontario when the annual number of cyclonic centres passing over an area is decreasing. During this time, the number of cyclonic passages in the late spring and summer is below average, and the majority of air masses involved in passages during these seasons are dry. They are of polar continental or polar maritime origin because a southward shift of the circulation pattern holds invasion of more southern air masses to a minimum.
>
> The required physical conditions for forest tent caterpillar population increase begin to occur with increasing frequency as the annual number of passing cyclones rises to a maximum. During this period of increase in cyclones, the number of passages during spring and summer is above average, and the majority of the air masses involved during these seasons are of south-western or southern origin because there is a northward shift of the circulation pattern which moves the more northern air masses to higher latitudes.'

Mortality factors

At each stage from egg to adult the spruce budworm is confronted by a variety of hazards. Food shortage, adverse weather, dispersal of young larvae and adults by wind, predators, parasites and diseases all take their toll. Quantitative studies of all these factors in relation to various forest types have been made in several regions during budworm outbreaks. For critical and well-documented reviews, the reader is again referred to Prebble (1954) and Prebble & Morris (1951). On the basis of data compiled during ecological studies at the Green River, N.B., field station, Morris & Miller (1954) have prepared life tables for the spruce budworm. This paper impresses me as one of first-class importance in the field of insect ecology. It will certainly facilitate refinements in comparisons between various control factors both within and between forest stand types and, hence, should add much to knowledge of forest management in relation to budworm control.

By means of rearing from material provided by the forest insect survey, and by special studies, extensive data on insect parasites of the budworm have been assembled. In British Columbia, Wilkes, Coppel & Mathers (1948) collected a total of forty-five primary and secondary parasites, of which fifteen were considered to be significant in relation to control.

McGugan (1951) has prepared, from published literature, a list of seventy species of parasitic insects and from his own investigations in Western Ontario has extended the list to seventy-seven. In the light of this and other extensive work, most of it as yet unpublished, the view prevails that in Eastern Canada, at least, parasites are unable to prevent or check an outbreak. Nevertheless, the evidence is clear that a decline, once started, is hastened by parasitism.

Concerning diseases of the budworm, a passing reference must suffice. An extensive programme of research is in progress at the Insect Pathology Laboratory, Sault Ste. Marie, Ontario. Three virus diseases, several fungous diseases and one caused by a protozoan are under study. None is of major consequence as a natural control factor. Studies of bacteria associated with the budworm have revealed nothing of ecological significance (Prebble, 1954).

Chemical control

The economic feasibility of protecting heavily infested stands from death by means of aerial applications of insecticides has been demonstrated in the State of Oregon and, more recently, in New Brunswick. In 1952, an area of about 300 square miles in northern New Brunswick was sprayed with DDT. Balch (1952) has described the organization and operation, and summarized the results. The area had suffered heavy defoliation for several years and the main objective was the preservation of valuable stands of timber. Larval mortality attributed to spraying was 99–100%. Extensive invasion of budworm moths from neighbouring areas resulted in widespread reinfestation of the treated area.

In 1953, an area of about 2800 square miles was sprayed. Results from the 2 years are described and discussed by Balch, Webb & Morris (1954). Satisfactory control was again achieved in 1953. In spite of reinfestation, the area sprayed in 1952 suffered less defoliation in 1953 than did unsprayed stands. It is concluded that protection of at least reasonably accessible stands is economically feasible.

So far as our present purpose is concerned, the significance of the spraying operations lies mainly in the opportunities provided for ecological study, and these are being exploited as fully as possible. Data are being accumulated with the purpose of throwing light on at least two important and interesting considerations. The first is the extent to which, if at all, the outbreak may be prolonged through interference with natural control factors. The second question concerns the possibility of increased frequency of outbreaks, resulting from climatic release, in mature stands that remain unharvested for relatively long periods.

In concluding this section, I wish to emphasize that this programme is designed to embrace all aspects of the ecology of the spruce budworm. Careful consideration has been given to the problem of balancing the fundamental and applied aspects of the work. It is already apparent that results of the fundamental researches in progress will contribute materially, and widely, to solving other problems of applied entomology in Canada and elsewhere.

Application of the results of ecological studies of the budworm problem in forest management practices will be a gradual process. The first advance over prevailing conditions will probably be the recognition of 'hazard areas', and orderly harvesting of the maturing crop in regions under commercial exploitation before destruction. Later advances may consist in deliberate attempts to reduce the likelihood of recurrent destructive outbreaks, through adoption of shorter rotations and frequent cutting cycles in pulpwood forests of Eastern Canada. The evidence for the belief that these measures will be effective is largely presumptive, or indirect, owing to lack of areas under intensive management for studies of the budworm problem at the present time. The belief will be proved or disproved only when critical studies of budworm populations are carried out in forests that, because of deliberate attempts to increase yield or to improve protection services, or simply as the result of continued periodic harvest cuttings, present a more varied forest cover and a more orderly assemblage of age-classes.

Conclusion

Trends in Canadian research in agriculture and forestry that have been developing for at least 25 years have become particularly apparent since the last World War. The development of research facilities in Canada, as elsewhere, was seriously retarded by the depression of the 'thirties and by the war. Since then, physical facilities have been enormously increased and improved, staffs have been expanded greatly and standards of training raised. Despite continuing weaknesses, there is evidence of increased attention to precise methods and appropriate experimental designs. However, I think that the most significant development is that of more comprehensive, long-term studies of major economic problems.

Most of our major problems are perennial, a fact inadequately appreciated by the general public and even by the non-biological scientist. Occasionally animal diseases can be eradicated, but they may, and do, return. We have yet to eradicate an economic insect that has become established and I believe the same is true for plant diseases. The effects of the use of toxic chemicals, of other farm and forestry practices, of climatic cycles, of ever-changing crop varieties and of the adaptability of insects and micro-organisms all serve to emphasize the necessity for increasing our understanding of the total ecology of farm crops, livestock and forests. This is not a simple matter. Modern buildings and complicated equipment, which we are accumulating rapidly, will not, useful as they are, provide the answers and I think there is convincing evidence that they will not be expected to.

I am indebted to Mr F. T. Lord for criticism of the section on orchard insects, to Dr C. H. Goulden for advice on the wheat genetics and breeding section and to Dr M. L. Prebble for invaluable help in the spruce budworm section. I am also obliged to Mr R. H. Wigmore for criticism of the entire manuscript.

REFERENCES

BALCH, R. E. (1952). The spruce budworm and aerial forest spraying. *Canad. geogr. J.* **45**, 201–9.

BALCH, R. E., WEBB, F. E. & MORRIS, R. F. (1954). Results of spraying against the spruce budworm in New Brunswick. *Forest Biology Division Bi-monthly Progress Report*, **10**, no. 1, 1–2.

BELYEA, R. M. (1952). Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part II. An assessment of the role of associated insect species in the death of severely weakened trees. *J. For.* **50**, 729–38.

BLAIS, J. R. (1952). The relationship of the spruce budworm (*Choristoneura fumiferana*, Clem.) to the flowering condition of balsam fir *Abies balsamea* (L.) Mill. *Canad. J. Zool.* **30**, 1–29.

BLAIS, J. R. (1954). The recurrence of spruce budworm infestations in the past century in the Lac Seul area of North-western Ontario. *Ecology*, **35**, 62–71.

DE GRYSE, J. J. (1947). Noxious forest insects and their control. *The Canada Yearbook*, pp. 389–400.

LARSON, R. I. (1952). Aneuploid analysis of inheritance of solid stem in common wheat. *Genetics*, **37**, 597–8.

LORD, F. T. (1947). The influence of spray programs on the fauna of apple orchards in Nova Scotia. II. Oystershell scale, *Lepidosaphes ulmi* (L.). *Canad. Ent.* **79**, 196–209.

LORD, F. T. (1949). The influence of spray programs on the fauna of apple orchards in Nova Scotia. Mites and their predators. *Canad. Ent.* **81**, 202–14, 217–30.

LORD, F. T. & MACPHEE, A. W. (1953). The influence of spray programs on the fauna of apple orchards in Nova Scotia. VI. Low temperatures and the natural control of the oystershell scale, *Lepidosaphes ulmi* (L.). *Canad. Ent.* **85**, 282–91.

MACPHEE, A. W. (1953). The influence of spray programs on the fauna of apple orchards in Nova Scotia. V. The predacious thrips, *Haplothrips faurei* Hood. *Canad. Ent.* **85**, 33–40.

MCGUGAN, B. M. (1951). Insect parasites of the spruce budworm in the Lake Nipigon area of Ontario. Ph.D. thesis, Univ. Wisconsin.

MILLER, H., EDGAR, J. & WHITESIDE, A. G. O. (1954). An improved small scale dough expansion test for the estimation of wheat quality. *Cereal Chem.* (in the Press).

MORRIS, R. F. (1951). The effects of flowering on the foliage production and growth of balsam fir. *For. Chron.* **27**, 40–57.

MORRIS, R. F. & MILLER, C. A. (1954). The development of life tables for the spruce budworm. *Canad. J. Zool.* **32**, 283–301.

PICKETT, A. D. & PATTERSON, N. A. (1953 [1954]). Observations on spray programs in 1953. *Proc. N.S. Fruit Growers' Ass.* pp. 31–6.

PICKETT, A. D., PATTERSON, N. A., STULTZ, H. T. & LORD, F. T. (1946). The influence of spray programs on the fauna of apple orchards in Nova Scotia. I. An appraisal of the problem and a method of approach. *Sci. Agric.* **26**, 590–600.

PLATT, A. W. & FARSTAD, C. W. (1952). The development of Rescue, the sawfly-resistant wheat. In *Agricultural Research in Canada*, pp. 47–51. The Agric. Inst. of Canada, Ottawa.

Prebble, M. L. (1954). Review of forest entomology in Canada. *Sixth Commonw. Ent. Conf.* London, England, July 1954.

Prebble, M. L. & Morris, R. F. (1951). Forest entomology in relation to silviculture in Canada. Part III. The spruce budworm problem. *For. Chron.* **27**, 14–22.

Sears, E. R. (1953). Nullisomic analysis in common wheat. *Amer. Nat.* **87**, 245–52.

Swaine, J. M., Craighead, F. C. & Bailey, I. W. (1924). Studies on the spruce budworm (*Cacoecia fumiferana* Clem.). *Bull. Canada Dep. Agric.* no. 37, N.S.

Thompson, W. P. (1949). Some problems in the cytogenetics of cereals. A historical review *Trans. roy. Soc. Can.* **43**, 35–44.

Turner, K. B. (1952). The relation of mortality of balsam fir, *Abies balsamea* (L.) Mill., caused by the spruce budworm, *Choristoneura fumiferana* (Clem.), to forest composition in the Algoma forest of Ontario. *Publ. Canad. Dep. Agric.* no. 875.

Wellington, W. G. (1952). Air-mass climatology of Ontario north of Lake Huron and Lake Superior before outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.), and the forest tent caterpillar, *Malacosoma disstria* Hbn. (Lepidoptera: Tortricidae, Lasiocampidae). *Canad. J. Zool.* **30**, 114–27.

Wellington, W. G., Fettes, J. J., Turner, K. B. & Belyea, R. M. (1950). Physical and biological indicators of the spruce budworm, *Choristoneura fumiferana* (Clem.). (Lepidoptera: Tortricidea). *Canad. J. Res.* D, **28**, 308–31.

Wilkes, A., Coppel, H. C. & Mathers, W. G. (1948). Notes on the insect parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.), in British Columbia. *Canad. Ent.* **80**, 138–55.

Unrau, J. (1950). The use of monosomes and nullisomes in cytogenetic studies of common wheat. *Sci. Agric.* **30**, 66–89.

International co-operation in the field of crop protection

Moore, W. C. (1955). *Ann. appl. Biol.* **42**, 67–72

THE DEVELOPMENT OF INTERNATIONAL CO-OPERATION IN CROP PROTECTION

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For very many years there have been plant pathologists—and I use the term in the widest sense—who have appreciated the need for some measure of international co-operation in combating plant diseases and pests, and who have struggled either individually or through scientific organizations to help satisfy the need. And if they were not strikingly successful before the Second World War it was certainly not for want of effort.

Now a great change has come about. There is a better appreciation of the important part played by pests and diseases in the struggle for efficient agricultural production; a highly competitive industry concerned with crop protection has grown up with astonishing rapidity; and an agreeable and close co-operation exists between industry and state organizations. Moreover, with present-day speed of travel, generous American financial aid and other facilities, many instead of few are able to see at first hand what is going on outside their own territory, either by taking part in conferences and missions, in attending training courses, or by paying personal visits. And many governmental and unofficial organizations have been set up which deal wholly or in part with one aspect or another of crop protection. An inevitable effect of all this activity has been the realization that control of pests and diseases must be a matter for international as well as national action. Indeed, so much activity has followed on this new climate of thought that there is a danger of the pendulum swinging too far the other way and of too hasty co-operation.

At the moment international collaboration in this field is still very much in the formative stage. Committees, Commissions or Working Parties of a bewildering number of bodies, familiarly known to the initiated under such names or initials as UNESCO, EPPO, CEZA, FATIS, O.E.E.C., F.A.O., I.L.O., W.H.O., B.T.O. and so on, are all trying to help solve one crop protection problem or another, but there is still much unconscious or conscious overlapping of effort. Gradually, however, confusion is giving way to method, and closer liaison between the different bodies is leading to a more rational division of functions. There is no doubt about the interest created among plant pathologists generally. Some years ago at least three 'First' International Congresses of Crop Protection were sponsored by different international groups. One of these has progressed to its third Congress and, despite the fact that it competes in part with the older Botanical and

Entomology Congresses, its membership is already so large that its value in achieving active and effective co-operation is more theoretical than practical. For practical results narrower specialization than that from Botany to Crop Protection seems necessary and there is already detectable a growing tendency towards relatively small inter-governmental or unofficial conferences on special subjects. These include meetings of specialists on particular pests or diseases at which the primary object is exchange of research information. There are, for instance, the two meetings already organized by the Netherlands on potato virus diseases, as well as the meetings of the Virus Sub-Committee of the International Institute for Sugar Beet Research. There are, too, the regional conferences called from time to time by F.A.O. or the European Plant Protection Organization (EPPO) to study such subjects as desert locust control, the problems of olive fly and fruit fly in Mediterranean countries, the musk rat in western Europe, potato root eelworm and so on, as well as the work of such bodies as the International Chestnut Commission recently set up to devise, among other things, effective methods of controlling Chestnut Blight, which has gained so firm a footing in southern Europe.

There would not be time to cover the whole field even if I knew it, and I can only quote a few examples to illustrate how progress is being made in a number of directions.

One obvious need is for co-operation on the regulatory side in preventing or hindering the spread of pests and diseases from country to country and continent to continent with planting material moving in international traffic. Certain basic requirements must be satisfied before there can be any hope of success in meeting this need. There must be in each country an efficient and trustworthy phytopathological service responsible for nursery inspections, for supervision over plant imports, and for intelligence work about the distribution and incidence of pests and diseases: prompt disclosure of information about new pests and diseases must be possible without fear of the immediate imposition of embargoes or stringent import regulations: plant import restrictions must be scientifically sound and designed to combine maximum security with minimum interference with trade: and each importing country must be in a position to know exactly what is meant or implied by the phytosanitary certificates or health declarations that accompany the plants or plant products it imports.

And yet, despite the difficulties these reservations evoke, it is on the regulatory side that greatest progress has probably been made so far. A conference, convened by the Netherlands Ministry of Agriculture in the spring of 1950 to discuss proposals for the improvement of international plant protection regulations, paved the way for the International Plant Protection Convention of 1951 sponsored by F.A.O. This Convention is a broad and flexible international agreement on basic principles which can be adapted to meet changing conditions and particular requirements. It encourages countries with rudimentary as well as those with highly developed plant protection services, and some forty countries have already accepted it. Under it each contracting government undertakes to collect and distribute information about plant pests and diseases occurring in its territory, to make phytosanitary inspections of growing plants and areas under cultivation, and to issue phytosanitary certificates which, when applied to planting material, shall conform with the standard or model certificate included in the Convention. Authority is given to regulate import of plants and plant products and to prescribe restrictions or regulations, provided they are based solely on phytosanitary grounds. Thus the machinery for achieving something of real value exists; and with it the hope that governments will enter into the spirit of things as well as paying lip service to ideals.

Provision was made in the Convention for supplementary agreements on common problems between countries located in the same geographical region, and for regional organizations to act as co-ordinating bodies. The European Plant Protection Organization (EPPO) was already in existence: it had been set up in 1950 as an autonomous and financially independent body, and a Convention embodying its constitution and functions was formally signed by the representatives of fifteen European governments in Paris in April 1951. It is recognized by F.A.O. as a regional organization serving Europe and already has much to its credit.

As far as regulations are concerned, small groups set up by EPPO have considered certain dangerous pests and diseases which have not yet reached Europe or which have only a limited foothold there, and have made recommendations on the best ways to prevent their introduction or further spread. They have also put on record the extent to which they consider restrictions are justified on purely scientific grounds in respect of four pests and diseases of major international importance—Colorado beetle, potato root eelworm, San José scale, and potato wart disease. There is nothing compulsory about these recommendations, but they are circulated to governments, and it is quite obvious that they are being accepted and in the main closely followed when existing legislation is revised.

It is hoped that similar regional organizations will follow elsewhere. One covering Africa south of the Sahara has been under discussion for some years, and efforts are being made to devise a limited agreement among countries in the South-East Asia area with a view to protecting that area from Leaf Blight (*Dothidella ulei*) of rubber and possibly one or two other non-indigenous diseases.

One difficulty about plant legislation is that of combining legality with understanding. Regulations must be so framed that they are proof against criticism in a court of law, and yet be capable of interpretation and understanding by ordinary people, including plant pathologists, exporters and importers in a number of countries. I have come to the conclusion that the two things are incompatible. Acts and Orders must be legal documents but can be kept as such. For everyday use a second document, not legally binding, but explaining and interpreting the regulations in everyday language would be of the greatest assistance in promoting the closer collaboration that is needed.

To turn for a moment to intelligence work and exchange of information about the occurrence of pests and diseases, I think that for general purposes this is a national matter and that national journals are the most appropriate media for publication. For established pests and diseases of international importance, and for new and potentially dangerous ones, a speedier, supplementary method of exchanging information is desirable, and the procedure adopted by EPPO is an admirable one. Information about certain major pests and diseases is collected at regular intervals, duplicated, and distributed at once: and a similar service is provided at irregular intervals for new diseases or in response to special requests from member countries. Facilities for a world reporting service have been provided by F.A.O. in their *Plant Protection Bulletin*, a monthly publication now in its second year. This is a useful medium, especially for those countries which as yet have no national outlet for intelligence information. It is also admirably suited for authoritative periodic reviews on the world or regional status of important pests and diseases, and for up-to-date information about national plant protection services and regulations about plants. As facilities for national publications improve these might indeed become its primary functions, even if publication were less frequent.

So much for collaboration in regulatory and intelligence work. A second and highly successful venture, at least in Europe, has been the development of co-ordinated schemes of field control. This began in 1947 with the setting up of an International Colorado Beetle Committee charged with the task of encouraging the plant protection services of western Europe to combine in an effort to check the further spread of Colorado beetle in Europe and to bring it under control in the countries already infested by it. Their efforts were so successful and so warmly appreciated that early in 1950 it was decided to extend the scope of the work to other important pests and diseases and to convert the Committee into the permanent independent body that is now called EPPO. Two of the Colorado beetle campaigns, in which EPPO, France, the Channel Islands and the United Kingdom have collaborated, are of particular interest to us. One, carried out for a number of years in the Cotentin peninsula of France, has served greatly to reduce if not overcome the risks of beetle invasion of the Channel Islands, which would threaten their trade with us. The other was in the Pas de Calais opposite our own south-eastern coast. But these are only two of many special campaigns initiated and organized by EPPO, and I will leave Dr Wilkins to tell us more about them, for he knows both the pain and pleasure they cause, and it is largely due to his energy and skill, first as Chairman of the 1947 Committee and later as Director-General of EPPO, that Europe has progressed so rapidly in this and other directions.

I should make brief mention here of the independent European Committee of Agricultural Zoology, familiarly called CEZA and presided over by Prof. Trouvelot, for among its functions it acts as an advisory body to EPPO on matters concerning research, and with the aid of grants it has been carrying out co-ordinated investigations on certain aspects of the biology of Colorado beetle, with particular reference to swarming and flights. The United Kingdom has contributed financially to this work, for being free from the beetle we are only too pleased to encourage research that may help us to maintain that freedom. A further example of this type of co-ordinated research is that begun last year into the biology and biological control of the Fall Webworm (*Hyphantria cunea*) in Austria and Yugoslavia, a project in which both EPPO and F.A.O. are actively interested.

Another development began with the setting up in 1951 of a UNESCO International Commission on Plant Disease Losses under the chairmanship of Dr Starr Chester. It took some time to get started, partly because of a desire to avoid overlapping with other bodies, but at a meeting held in Paris in July last the Commission decided to confine its attention to collaborative work and exchange of information on *methods* for assessing accurately the damage caused by diseases. This, as far as I am aware, is not being covered by any other organization, and it is a subject we shall hear more about later in the week.

Pesticides provide my last example of development in international collaboration and it is a very topical one, especially as regards standardizing names and labels, devising an international approval scheme, and agreeing on the safety precautions to be applied in handling and using toxic chemicals. Here, however, is an instance where considerable confusion still reigns, for at least five international bodies are independently engaged in discussing the matter and so far there is little sign either of co-ordination of effort or of any attempt to pick out and concentrate on the problems that show at least some promise of early solution. Agreed common names for chemicals is a worthy object, especially if the choice is based on some general principles and is not haphazard. This problem is being tackled both in this country and America and it is hoped to co-ordinate the work through the newly established International Standards Organization. I think it would also be a boon if there were uniformity in naming proprietary pesticides sold in different countries.

The difficult problem of labelling dangerous and toxic chemicals, including those used in agriculture, has been the subject of a number of wide and fruitless discussions by different bodies. The International Labour Office, however, has taken a narrower and more realistic line. They have recognized that if those people of different nationalities who have to handle goods moving in international traffic are to distinguish between explosive, flammable, corrosive and toxic chemicals the labels must be few in number and words must be avoided. As a result they have already made much useful progress in devising symbols for the identification of dangerous substances in transit.

The latest attempt is aimed at agreements about toxicity of pesticides, with a view to preparing lists of materials to be prohibited or tolerated, and laying down maximum contents and residue tolerances. So little is known about this subject, however, that in my view the important thing for the present is for countries to press forward with research in order to obtain the basic information required, and to confine collaboration to the exchange of that information. Nor would there appear to be much prospect at present of devising a single acceptable international approval scheme. On the other hand, there is much to be said for seeking agreement about specifications and standard methods of analysis for pesticides wherever that is possible.

I fear my treatment of the subject has been very sketchy and incomplete but I have probably said enough at least to justify my assertion that a great change has come about in this particular field of work since pre-war days.

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INTERNATIONAL CO-OPERATION IN ACTION

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This paper deals only with Europe and the Mediterranean area, and is concerned with the activities of the European Plant Protection Organization, which was established by a Convention signed in Paris in April 1951.

The origin of the scheme can be traced to the autumn of 1947, when certain countries in western Europe decided to take joint action in an effort to control the Colorado beetle. This pest had spread greatly in Europe during the war of 1939–45, and there was a tendency in some countries to regard effective control as impossible. On the other hand, some countries, including Great Britain, Ireland and the Scandinavian area, were still uninfested, and were anxious to remain so. In consequence, severe restrictions were imposed by them on the importation of produce, particularly vegetables and potatoes, likely to carry beetles. These restrictions had the effect of virtually closing the British market to imports of salad vegetables, early potatoes, etc. from European countries from March onwards, which was a serious matter for several countries, particularly the Netherlands, Belgium, France and Italy. It was with this background that the International Colorado Beetle Committee—an informal inter-governmental body—was established late in 1947, resolved to foster co-ordinated action between the plant protection services of western European governments, to see if by this means it would be possible to bring the beetle under control in the infested countries, and prevent it from spreading to countries that were still free.

The committee started work in 1948 with an initial fund of about £100,000, contributed mainly by the governments of the United Kingdom, the Netherlands and Ireland. In that year the plant protection services of France, Belgium, the Netherlands, Luxembourg and Western Germany (through the Allied Control Commission) co-operated in a spraying scheme under which all potato crops within 20 km. from their frontiers were treated against Colorado beetle. Technically this was not the best approach to the problem, but it had excellent propaganda value, and succeeded in drawing a large measure of public attention to the economic importance of the pest. In 1949 a large potato spraying demonstration, involving the use of helicopters, fixed-wing aircraft, and many types of ground spraying machines, was organized near Caen, Normandy. Following this, and in subsequent years, co-ordinated spraying campaigns have been in progress in several areas regarded as of special importance, namely the Cotentin peninsula (to protect the

Channel Islands), the Pas-de-Calais and Nord Departments of France, the northern kreise of Schleswig-Holstein (to protect Denmark), eastern Bavaria (to protect Austria and Czechoslovakia), and the frontier region of Italy near her frontiers with Austria and Yugoslavia. Among propaganda measures may be mentioned the production of an international Colorado beetle film, in two sizes and three languages, which has been widely shown in most European countries. Finally, reports on the beetle position in Europe have been collected at frequent intervals during each season and distributed to the various plant protection services.

The combined effect of these various measures has undoubtedly been to stir up the interest of governments in a more effective control of the pest.

In spite of the fears that prevailed in 1947, there has been no further spread of the beetle to countries west and north of the then-infested area. In so far as this is a reflexion of the increased interest taken in controlling the pest, under the stimulus provided by friendly co-ordination of effort, the experiment in international collaboration which was set on foot in 1947 has proved well worth-while.

As the work of the Committee progressed, and it became evident that in the field of plant protection active collaboration between nations was not only practicable but was warmly appreciated, the feeling gained ground among experts and administrators alike that the Committee should expand its functions to cover other pests and diseases, particularly those interfering with international trade in foodstuffs. This led to the decision, taken at an international conference convened in Florence in January 1950, to re-name the Committee the European Plant Protection Organization, and to extend its scope to cover other pests and diseases of international importance, including those infesting stored foodstuffs. A draft Convention designed to establish the Organization on a formal inter-governmental basis was considered at an international congress convened by the Dutch Government and FAO in The Hague in April 1950, and this Convention was signed in Paris—as indicated in the first paragraph of this paper—in April 1951. Twenty European and Mediterranean governments are now members, and others are expected to join.

The policy followed has been that while EPPO is interested in all pests and diseases, particularly those which affect international trade, special attention should be paid to a limited number of general interest throughout Europe. The original list, incorporated in a schedule to the 1951 Convention, comprised Colorado beetle, potato root eelworm, San José scale, potato wart disease, the pests and diseases of stored foodstuffs, and rodent pests of crops. To this list the fall webworm (*Hyphantria cunea*) was added in 1952. Much attention has also been paid to the pests and diseases of special interest to the Mediterranean countries, particularly the Mediterranean fruit fly. It is not possible in a short paper to describe adequately all that has been achieved in this very wide field of activity, but any who are interested may obtain copies of EPPO publications and progress reports by applying to the address given at the head of this paper.

Mention should be made of the reporting service. The Organization is recognized by FAO as the regional plant protection organization for Europe under the terms of the International Plant Protection Convention signed in Rome in 1951, and its European reporting service has been integrated with the world reporting service of FAO. Reports considered to be of general interest are distributed throughout the year in the two official languages of the Organization, English and French. In addition, annual reports are prepared and circulated on the main pests and diseases mentioned in the preceding paragraph; various special inquiries have also been made at the request of individual governments, and the results collated and distributed.

It will be seen that in less than 7 years an active and successful plant protection organization has been founded in Europe. Perhaps the main reason for its success is the fact that it started with one pest only, and its later expansion was founded on the mutual confidence established in dealing with that pest. In the case of large organizations with a political background, such as those that are linked with the United Nations, it is possible to have wide terms of reference from the outset; but with small bodies such as EPPO, technical in character and entirely non-political, where quick action and value-for-money are essential factors in winning esteem and support, the wise course is to begin in a small way and expand in the light of experience.

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BARRIERS AND BY-PASSES IN PLANT TRADE

By E. GRAM

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Tourists and other travellers will admit that passing from one country to another has been greatly facilitated in recent years. When some enthusiastic globe-trotter describes, in a letter to the editor, how he dug up a small oak tree as a souvenir of his last picnic-place, only to have it confiscated at the frontier of his native land, one's first reaction is to exclaim with the correspondent 'What a lot of nonsense!'—unless, by chance, the reader feels some sort of paternal responsibility which induces him to defend measures designed to keep out diseases and pests. It would seem that regulations are not always appreciated, for even those whom they are intended to benefit are oft-times somewhat sceptical.

The barring of the way to pests and diseases requires elaborate arrangements. It is no simple matter—as we all know. On the other hand, it is not an impossibility. There is, on every highroad crossing the frontier of California, a quarantine station, outside which may be seen families doggedly consuming that bag of apples which they are forbidden to carry into the state without the necessary precautions having been taken. The amount of contraband intercepted when transatlantic clippers arrive at New York is amazing, the carloads brought by the passengers of certain liners is quite overwhelming—while the museum of dangerous specimens found must be seen to be believed. Even here in Europe international intercourse is not entirely innocent.

Illegal trade and carelessness in private traffic is far more dangerous than one might suppose. It is, perhaps, a myth that potato wart was first carried from Europe to the U.S.A. with potatoes pocketed away in the bundles of immigrating miners; there may be something in the theory that potato root nematode was introduced to America by way of ships' ballast, illegally consisting of soil instead of gravel, and subsequently dumped on Long Island. Be that as it may, it is officially admitted that a serious first infestation with San José scale was smuggled into Germany with fruit trees imported in violation of Customs and sanitary regulations. The first potato nematode localities in Denmark occurred—strangely enough—in the vicinity of small sea ports; anyone observing crates of potatoes being landed—illegally and thoughtlessly—from small boats is at liberty to draw his own conclusions.

In practically all countries legal trade is complying with those regulations which aim—more or less directly—at the important diseases and pests. The country with the lowest threshold, therefore, is liable to become a dumping ground for articles of poor quality and doubtful health. We have but to recall such pests as Colorado beetle and San José scale, or such diseases as Chestnut Blight, Oak Wilt and Potato Spindle Tuber—and we shall all agree that to keep these and similar horrors out of continents or regions hitherto free, is well worth some inconvenience and expense. Tourists who import numbers of living Colorado beetles just for the fun of it—or even for educational purposes—richly deserve whatever punishment or inconvenience is meted out to them at the frontier. Some regulations may appear absurd, while a few bear witness to an extensive, albeit unseasoned knowledge of printed matter. If we add ignorance of human nature and man's unfailing ability to discover a loophole we get a situation which—to say the least—is 'tiresome'. When quarantine is maintained against a presumed bacteriosis, later ascribed to boron deficiency, we may decry it as absurd or obsolete—but let us rather look nearer home and remember the rules for export directly from the place of production, even where grading stations and packing centres keep a severe eye open for disease and pest. We have no difficulty in understanding those countries which require that potatoes be sacked—*not* on the farm—but at the harbour.

If the introduction of Oak Wilt is feared an embargo placed on oak trees would seem to be a very simple solution. It will, however, soon be found necessary to appoint an inspector who knows an oak tree from related plants—not to mention that our excellent geneticists and breeders will need oaks from places that are not entirely reassuring. And by the way—how long dare we continue to import interesting but little known plants from the back of beyond without one or more European quarantine nurseries? Many plants and parts of plants must, in any case, be imported, in spite of a certain risk. Therefore In-port inspection is a well-known feature, although expense and delay are, of necessity, incurred. The lists of parasites intercepted show that ocular inspection is no mere formality; in many cases, however—notably among the viroses—detention is called for, often lasting a season or possibly two seasons. In special cases this period may be reduced to a fortnight or even 24 hours, thanks to modern virus technique.

Most importing countries require an Out-port inspection; obviously the exporting country also stands to gain by this, for any country will be anxious to guard the reputation of its products, and while an inspection before packing has all the possibilities of being efficient the existence of an inspection immediately before loading has, in actual fact, improved quality. The influence of proper packing on quality—especially from the point of view of the buyer—is important; and the incongruity of healthy plants packed in infested straw, dirty sacks, or unstripped wood can be stopped. The ideal—that a plant inspector from the importing country should co-operate right from Out-port inspection, thus making most In-port inspection superfluous—would be welcomed by all airlines and shipping companies. When a cargo of potatoes is loaded for export the critical representative of the buyer will be on the quay. Why not the phytosanitary inspector of the importing country? Inspectors from the U.S.A. have, in fact, accepted invitations to do their work abroad. Thus officers will meet and a knowledge of each other's ways may help to simplify matters.

Rationalize is, perhaps, a happier term than simplify—the postulated simplicity of an embargo being our last resort—or the first resort in cases of suspected peril, until the evil and its prevention is better known.

In the production of seed potatoes field inspection of the growing plants is a fixed tradition but the technique is under continual development, improved on the one hand by increasing pedigree propagation (clones), and on the other by serological and chemical tests, eye indexing, and control samples planted in greenhouses or fields in the South shortly after harvest. Virus, the ever-present thorn in the side of potato culture, has necessitated also the more or less compulsory field inspection of nurseries, notably of fruit bushes, bulbs and strawberry plants. Some years ago the Nurserymen's Union in my country came to the Plant Inspection Service and applied *en bloc* for inspection of all their nurseries, as if they all were going in for export. That demand has developed into a National Committee for Propagation and Sanitary Inspection of Horticultural Plants; that this committee was formed by the buyers' and producers' several organizations—in close touch, nevertheless, with official research and inspection—has been the means of smoothing out some common difficulties. An adequate number of highly qualified inspectors must be available always, sufficient even for the rush seasons—but not too many government officials loitering around with too little to do—and worse still, becoming overzealous. Here work with pedigree stock in the case of raspberries, strawberries and a few other species combined with a general field inspection of all nurseries has proved convenient. Voluntary inspection, aiming at a National Market, appears to tighten up—without undue harshness—the compulsory field inspection required with export. Our nurserymen are winning respect. Last year their Union asked to have all their sections sampled for potato root eelworm; they had their reward when we found but two samples containing cysts—out of about 1900 tested.

The cost of field inspection is easily calculated and it is the first point to crop up when further inspection comes under discussion. The returns can be entered on several accounts; one being the certainty of advice regarding control measures, another the indispensability of thorough sanitation given at home when we aim at rationalization of international regulations. The contrary is, however, most unfortunate, that is to say when the economic spiral is started in reverse and plant trade is obstructed to such a degree that no margin is left for control expenses.

In the seed potato trade individual containers bear as indication of origin the growers number, even though the potatoes are passed through a grading centre. Individual fruit trees and bundles of bushes may be marked in the same way. Flower bulbs, corms, some seeds or fruits from different growers are pooled and graded, being marked by the grading centre only. This may mean, however, that if one of these products is liable to carry dangerous diseases the fields must be inspected at the appropriate time and products from rejected sections will be excluded. Most fruits and seeds are, as a rule, marked with the name of the grading firm, only; table potatoes for export fall into one or the other of the two last-named categories.

It is a traditional right of nurserymen to supplement orders with plants from other nurseries without giving any indication of this to the unsuspecting buyer. But various plant inspection measures put a spoke in the wheel of such tactics. And indeed, if some new or rare disease is discovered after delivery it may be of more than academic interest to trace the case back to the grower and the inspector responsible. On the other hand, provided all nurseries and plant dealers' premises are thoroughly inspected at the proper times and provided, also, all rejected lots are properly disposed of, it ought to be lawful for nurserymen in such a district to pool and grade their products. One might perhaps compromise by extending the marking of individual trees and bundles. It is perfectly understandable that an exporter would not care to let his provider and his customer come into too close contact with each other, but this can be avoided by the use of secret key numbers to indicate the source of supply. Such pooling is not, however, a purely national matter; it implies that the importing country feels such confidence in the inspection system of the exporting country that it is willing to accept the name of an entire district as sufficient declaration of origin. With the methods now available for the detecting of nematode cysts and potato wart sporangia in the soil two barriers to free intercourse between nurseries seem to be eliminated. How much more satisfactory it is to be able to say that a nursery has been definitely searched for potato wart sporangia than to go on the assumption that there is none, merely because one has the negative information that none has been reported within a radius of 5 or 20 kilometres.

We all aim at sound quarantine regulations, based on biological knowledge, but the range of dangerous pests and diseases may impede simplicity and the same thing is true of cultural and trade practices. We know that there are certain regions particularly suited to the production of certain seeds—but the range of some seed-transmitted disease (e.g. lettuce mosaic) may include that self-same favourable region. Flower bulbs may, with advantage, be started in one country, grown for one or more seasons in another, and finally be exported directly from the adopted country or from the original home. We have no desire to see ghosts in broad daylight but certain forebodings are justified in such cases. When a nursery makes root-graftings on stock from some other nursery specializing in this culture, using grafts from yet a third place, one begins to feel that the whole business was simply invented to tease scrupulous plant inspection officers. The latter know that growers are opposed to law-breaking, but they also know that there are consciences—and consciences!

A study of the range of really dangerous diseases and pests ought to result in a rationalization of regulations—a successive smoothing out of discrepancies—at least between neighbouring countries. We know of cases in which even the name of the grower and the holding is required by importing countries, yet doubtless Europe would sometimes be sufficient declaration of origin.

A staff of trained inspectors cultivating the detective sport do—surprisingly often—find a needle in a haystack. The crucial moment is when the inspector is asked to certify the absence of any needle! We may still find, in regulations, statements required which nobody can possibly sign without some mental reservations. Not only is the protection of plants a matter of importance: we must also consider those men who are required to sign documents. In view of the immense development of pesticides disinfection might remove a part of this difficulty. An infection of less than one per thousand of the seeds with *Phoma napobrassicae* may—by means of secondary infections—give rise to large patches in a swede field should that particular variety be susceptible. Such a case is by no means unique. With all due regard to the possibility of detecting such infections in the laboratory a good seed disinfection may prove more reliable and cause less delay to the trade. We know so much about fumigation against San José scale that fumigation nowadays competes favourably with a fully adequate ocular inspection; when the services are in close contact with each other it will always be possible to select the most suitable place for fumigation to be carried out—at the nursery, Out-port or In-port. Large quantities of cotton, tobacco, etc., are fumigated in ports on arrival, but the disinfestation of grain remains as one of the toughest problems before us; a good deal of grain might be saved from damage—and a good deal of ship fumigation avoided —if no infested grain were passed from export harbours to ships' holds.

Seed treatment as a practical measure is widely applied in agriculture but there is still much experimental work to be tackled before we can obtain any really significant relief for international seed trade. The tolerance of different species, the susceptibility of individual seed lots, the storage of treated seed, the selection of wide-ranging pesticides—all these points call for teamwork between the laboratories and for an international balance-sheet.

Another knotty point is the treatment of plants with roots which may carry all kinds of undesirable organisms. We might, however, find something better than the rather brutal spraying which is carried on until all the soil—and with it many tender rootlets—is washed away. Here again teamwork between nurseries and laboratories is needed. It is merely to by-pass the question when Norway and Denmark decide to dispense with the strict freedom-from-soil rules, because the two countries run about even in the matter of soil-borne pests. The importance of surveys for such moderating decisions can only be touched upon; probably all responsible officers now adhere to the practice of openly reporting all diseases and pests found; those still in favour of secrecy—which pretends to serve the interests of the trade—will learn to know the distrust shown to any country which winks at an important attack. Moreover, surveys are the solid foundation of public interference; the private grower will control an attack only so far as his pocket and pleasure are concerned—the encouraging history of the Colorado beetle in England proves the indispensability of a broader view and a longer purse.

When finance enters the picture—if not before—we are bound to answer the question: Is plant quarantine in general worth while? University departments teaching foresight are still a dream. Nobody could have foreseen that the extending of potato growing to the virgin prairies of Nebraska and Colorado would open the door of whole continents to a small beetle, subsisting hitherto on wild *Solani* in the foothills; that the introduction of healthy pines from America to Europe would establish a devastating rust; or that European sheep—blameless from a veterinarian point of view—would carry in their wool seeds of grasses and clovers new to Australia. It makes one shudder to think of the fungi, bacteria, viruses and insects that clover seed in particular may harbour. Furthermore, it is said, we are helpless against the natural drift of insects and fungus spores. But we are not! Grasshopper control in the South as well as Colorado beetle control in the North definitely contradict this defeatist attitude. Even the stopping of long-range drift of rust spores may not be entirely beyond us; changes of cultural practices at the source of the trouble are being investigated in the East as well as in the West. Let us, therefore, frankly admit our shortcomings and take what steps we can to eliminate some of them. Air traffic and world trade in grain are among those things that would bear investigation for a start. We cannot make any definite promise to exclude utterly any given pest but we have proved ourselves able to postpone invasions, thus saving for many years the expense of an all-over direct control; we have suppressed attacks, thereby raising the morale of farmers and inspection officers; we have shown that we are capable of securing a respite for the development of chemical control and of resistant varieties. We are aware that a new and dangerous type of potato wart is lurking in the offing—but we do know it. And what is more our breeders know it.

The economic effect of quarantine measures would fill a hand-book. Here I shall mention but one outgrowth—as a kind of obituary, I hope. Plant quarantine is rarely discussed until someone hints at protectionism. We may still find ourselves being asked to point to some pest which can serve as scape-goat—the fine-sounding reason for stopping the import of some tropical fruit or other, when the real reason lies in the dabbler's inability to sell his own worm-eaten product! But in an era when most governments more or less openly direct their sales and purchases this danger of abusing quarantine is, I feel, dwindling.

It is the duty of each of the phytosanitary services to protect their own country; in order to do this it may be necessary to bar certain plant transports. It is a far happier task to open up new roads—and this will, naturally, involve a certain development of the inspection of growing plants and of the disinfection of seed and other propagation material. Starting at home, bringing internal inspection and control up to standard, it should be possible to simplify quarantine procedure, abrogating some requirements, bringing others into line at least between neighbouring countries with identical fears and woes. All this must be a matter of time and patience—but it must not be lost sight of. Seeking the happy medium between liberty and discipline we await—and confidently expect—valuable inspiration from our colleagues in the Association of Applied Biologists.

Insect pests of stored products

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PROBLEMS OF FOOD STORAGE IN TROPICAL TERRITORIES

By D. W. HALL

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(With 1 Text-figure)

Introduction

Interest in the losses to foodstuffs during storage in temperate climates has been comparatively recent, and investigation into the factors causing such losses has occupied the serious attention of scientists only for the past twenty years. In tropical countries, with the exception of the enthusiasm of one or two government entomologists since 1935, planned research and control started about five years ago.

The pioneer work in stored products entomology of Prof. J. W. Munro cannot be over-emphasized, and it is through his work, and also more recently through the work of Mr G. V. B. Herford and others, that official cognizance is now being taken of the necessity to accelerate (and in very many cases to start) improvements in methods of storing foodstuffs in tropical territories. It was as a result of their efforts that a tour of East and Central Africa was made by T. A. Oxley, of the Department of Scientific and Industrial Research, Pest Infestation Laboratory, in 1949, to advise on grain storage. Recently, further official action has been taken by the Colonial Office and the Department of Scientific and Industrial Research by the appointment in 1951 to the Pest Infestation Laboratory of a Colonial Liaison Officer who is concerned with the development of the study of food storage problems in colonial territories and with improving storage methods in these territories. I feel very honoured that this work should have fallen to me.

Importance of the storage problem

In 1946 a committee of the U.N. Food and Agriculture Organization estimated that the overall loss during storage in temperate and tropical parts of the world to grain, pulses and oilseeds might be 10%. This estimate included losses caused by insects, rodents and fungi.

A detailed survey to determine losses to foodstuffs during storage in tropical territories has not been made, but from information being slowly collected about losses due to insects only, it is now fairly obvious that the assumed losses figure for tropical territories used to arrive at the above average, is an underestimate. This is not surprising because conditions in tropical countries are conducive to greater losses in storage than conditions in temperate countries and accurate assessments are not obtainable because of the complexity of the assessment, and because reliable records have not been kept.

During the past five years small pieces of information about losses in storage have been collected from a number of sources in tropical territories in an attempt to obtain an indication of extent of losses or the effectiveness or otherwise of control measures which may have been carried out. These are summarized in Table 1. The figures given are not to be regarded as accurate assessments of losses but more as enlightened estimates. Those given by the farmer or Government Department concerned are almost certainly underestimates as indicated in case 2 by the loss of 14% when insects, frass, etc., were sieved and carefully dissected out as compared with the rough overall loss of 3% as estimated by the difference in weight between intake and delivery (see also cases 4 and 8). It is interesting to compare cases 2 and 4 and to see that as a result of adopting control measures—dusting each layer of bags with BHC dust and building large tight stacks which promoted self-sterilization of the stacks and gave conditions of maximum efficiency for the BHC by reducing air movement within the stack—losses in maize storage were reduced by 50% which resulted in an estimated saving of £50,000.

Loss, from inefficient milling of a commodity, as a result of insect attack is indicated by the data (case 7) given for paddy storage in Table 1. Paddy which has supported one or two generations of insects such as *Sitotroga cerealella*, *Rhizopertha dominica* and *Calandra oryzae* when put through a huller is milled into a larger percentage of 'brokens' than it would have if it had not been infested during storage. The miller thus gets probably 40 lb. of good grade rice instead of 60 lb. from 100 lb. of paddy.

Table 1 also indicates the importance of insect attack in causing an increase in the acidity of an oilseed such as groundnuts (cases 13 and 14). This results in considerable financial loss because the acid oil has a lower market price than the natural oil, and also a commodity is manufactured from it which has a lower price than that manufactured from the good oil.

Much of the temperate zone must import foodstuffs from the tropical regions, and the United Kingdom is no exception. It is obvious that the conditions of storage prior to import into the temperate country are extremely important. The fact that foodstuff has been exposed and subjected to infestation at any post-harvest period may cause loss to the exporting country in ways other than direct weight loss. This is especially so if the importing country has very strict food laws (e.g. America) maintained by analytical tests which detect the presence of fragments of insect chitin and rodent hairs. By such tests it is possible to detect if the foodstuff has been exposed to insect or rodent infestation at any period after it was harvested. These tests apart, all countries are now less willing to purchase for human consumption food which can be seen to be infested with insects. Also, infestation in a tropical country's produce may necessitate the purchase by the importing country

TABLE I. *Examples of storage losses collected from a number of sources in British tropical territories*

Case no.	Commodity product	Storage conditions	Storage period in months	Estimate of loss by percentage breakage above normal	Estimate of loss by weight difference: Straight (%)	Estimate of loss by weight difference: After insects, dust, faeces removed (%)	Estimate of loss: By increase in acidity of oil (%)	Estimate of loss: By damaged grains (%)	Estimate of equivalent loss of commodity	Estimate of equivalent financial loss
1	Maize	Primitive. Corrugated iron sheds. No dunnage. No control measures. Poor stacking	12	—	17	—	—	—	12,000 bags maize in one area	£24,000
2	Maize	Hanger-type premises. No control measures. Loose stacking	12	—	3–4	14	—	—	53,000–63,000 bags maize in a territory	£75,000
3	Maize	Hanger-type. Dunnage. Large tight stacks	12	—	—	—	—	—	21,000 bags maize in a territory	£32,000
4	Maize	Bags dusted with BHC	12	—	1·6–2·0	6	—	—	30,000 bags maize in a territory	£50,000–£70,000
5	Maize	In native-type cribs. Stored on cob with sheath	12	—	15	—	—	—	—	—
6	Padi	Dilapidated corrugated iron shed. Dunnage	6	—	2·5	—	—	—	12 tons padi	1300 $ B.W.I. £270
7	Padi	Good premises. No control measures	—	30	—	—	—	—	—	—
8	Rough rice	Corrugated iron shed. Dunnage	12	—	4–5	14–15	—	—	—	—
9	Wheat	Bulk within bagged bulk-heads	—	—	5	—	—	—	200 tons wheat	£60,000
10	Groundnuts	Undecorticated in bags in warehouse premises	9	—	—	—	—	16·3	270 tons nuts	£14,700
11	Groundnuts	Undecorticated in bulk in open-type and closed style seccos	9	—	—	—	—	2·4–16 (av. 5)	1,650 tons of nuts or 1400 tons of oil	£90,050 £150,000
12	Groundnuts	Undecorticated in bulk during shipment	—	—	—	—	—	2–3 %	0·6–1·4 % of oil present	
13	Groundnuts	Decorticated nuts in bags in pyramids	12	—	—	—	Whole nuts 4 % Splits 9 % Brokens 70 %	—	—	—
14	Groundnuts	Decorticated nuts in bags in pyramids	12–18	—	—	—	3·5	—	9000 tons margarine	—
15	Groundnuts	Decorticated nuts	2	—	—	—	Loss in extractable protein 1·8–3·9 %	—	—	—

of the same commodity from a temperate country at higher price, e.g. the United Kingdom has to purchase haricot beans from the United States because the beans from the Colonies are infested with Bruchids. Thus with increased competition in world trade exporting countries must take every precaution to ensure that their export crops are properly stored.

In tropical countries, no less than elsewhere, insects do not confine their attentions only to foodstuffs for export. Thus all foodstuffs within a territory must be looked after and infestation prevented. In certain tropical territories, where the health of a village is dependent on one or two commodities which are susceptible to infestation during storage in the native cribs, the nutritional value of the diet may be so impaired that malnutrition results, e.g. cowpeas, maize, and sorghum can be so heavily infested with Bruchids and weevils that very little but the insects and the outer skin of the grain are left. In Africa the staple diet of the African is maize meal. Maize, from local stores and from native cribs, infested with insects, is poured straight into a hammer mill and maize, insects, etc., are ground up into meal. Recent tests on certain samples of meal from Africa have indicated that the meal consumed contained up to 20,000 insect fragments and up to 20 rodent hairs per 25 g. of meal. Since the introduction of the hammer mill I understand there have been many more complaints of digestive troubles and it is obvious there is an urgent need for the improvement of storage methods.

There is one other important aspect. If stored-product insect pests are not controlled they will continue to spread throughout the world by trade, e.g. *Laemophloeus pusilloides*, originally found in South America and Australia, has recently been found in Africa.

There are therefore four reasons why the problems of food storage should be tackled in tropical territories as well as in an importing country such as the United Kingdom:

(1) To reduce losses in quantity of commodity between time of harvest and arrival in the importing country.

(2) To improve the quality of the commodity for consumption in the importing country.

(3) To improve the quality and increase the quantity of the commodity consumed in its territory of origin.

(4) To prevent the replenishment of the stored product insect fauna in the importing country and the spread of insects into new countries.

ANALYSIS OF THE PROBLEM

The problem of food storage is one of the action of physical, chemical, and biological factors on each other and on the commodity stored. It is very complex, and an attempt at analysis has been made in Fig. 1. This suggests that the two main influencing factors are science and the sociological and economic conditions.

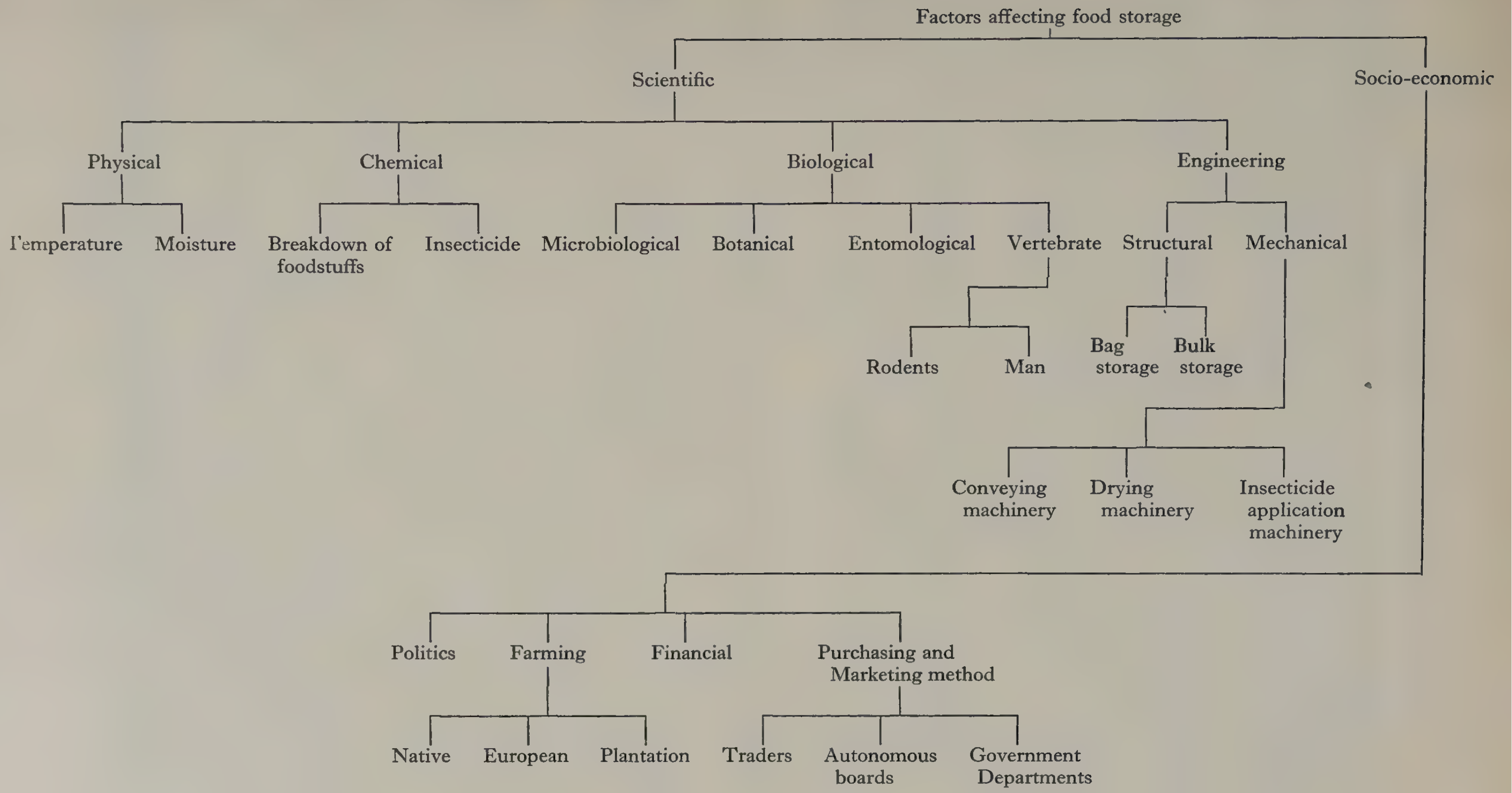
Factors affecting food storage
Scientific
Socio-economic
Physical
Chemical
Biological
Engineering
Temperature
Moisture
Breakdown of foodstuffs
Insecticide
Microbiological
Botanical
Entomological
Vertebrate
Structural
Mechanical
Rodents
Man
Bag storage
Bulk storage
Conveying machinery
Drying machinery
Insecticide application machinery
Politics
Farming
Financial
Purchasing and Marketing method
Native
European
Plantation
Traders
Autonomous boards
Government Departments

Fig. 1. Analysis of problem of food storage.

Many scientific data of a biological, chemical and physical nature already exist about the behaviour of insects, chemicals and stored foodstuffs under certain temperature and humidity conditions typical of temperate climates. Very little comparable scientific information has been obtained from tropical climates and the problem has not been assessed in detail.

There is a general lack of information on the importance of the species of insect pests and on their biology under tropical conditions, and only in a few countries is there information on the species and importance of rodent pests in both urban areas (where the problem is universal) and rural areas (where the problem is regional). Until reliable information is obtained about the troublesome species, attempts at control will not be successful because the behaviour of insects, rodents, foodstuffs and chemicals is different under tropical conditions and temperate conditions.

Microbiological problems associated with storage under tropical conditions are even less well understood. The importance of fungi in relation to moisture content of the commodity and to temperature is a major aspect in those territories where crops are harvested during or immediately prior to rains.

This sombre situation is due to a combination of factors of which probably the most important are:

(1) Shortage of money.

(2) A lack of appreciation on the part of administrators of the extent and importance of losses and of the need, in advance, for research work.

(3) An ever increasing volume of routine and advisory work for the specialist.

(4) The tremendous delay between ordering and receiving vital equipment making any but the most preliminary experimentation impossible.

(5) The lack of appreciation of tropical requirements by most manufacturers of equipment for handling and storing foodstuffs.

Since governments are generally unwilling to devote money to a problem unless they can be given figures to prove that it is of economic importance, the scientist is confronted with a galling situation because the figures needed can be sought only by careful surveys and investigations which themselves require money.

When fundamental information on the interaction of both physical and chemical factors on the commodity stored and on the troublesome agent has been obtained, there is then an applied research problem, i.e. a major practical problem of developing field methods which make use of the fundamental information already available. Too little attention has been paid in the past to the importance of engineering knowledge in this field of work, particularly, I think, with reference to construction of buildings and machinery specially designed to store and handle foodstuffs in the best possible way.

In tropical territories, probably more than anywhere else, foodstuffs have been stored in any type of building available. Very large quantities of foodstuffs have been lost for human consumption because the storage building used was not weather, insect, bird and man-proof; could not be sealed for fumigation; had a floor surface which was permeable to dampness; and had endemic infestations in many ledges, cracks and crevices where it was extremely difficult to kill pests. The type of construction desirable depends partly on climatic conditions and therefore careful consideration must be given to this; e.g. if a dry commodity is to be stored in an area of high humidity then the storage structure should have minimum ventilation such as is obtained with closed metal or concrete silos; whereas if a damp commodity is to be stored in an area of low humidity storage should be in a well-ventilated building or in silos fitted for circulation. In many parts of the world storage structures should be such that both maximum and minimum ventilation can be obtained, and new ideas for cheap efficient storage structures are needed.

Mechanical engineering too has a challenge to face. Very few machines for handling and drying commodities have been constructed robust and simple enough for use in tropical countries where, because of the distance from technical 'know how' and the lack of local technical skill, it is essential that breakdowns should be minimal. Similarly, with machines for dispersing insecticides either as fumigants, sprays, or dusts, robustness, cheapness and simplicity combined with efficiency are the prime factors. In certain cases territories have not carried out any control measures because of the inability to obtain a machine which would stand up to the local climatic and human factors.

Even when these problems have been solved there is the final overriding local factor, which I call the Socio-Economic factor, which unless radically changed or altered may retard a satisfactory solution to the problem. The problem of storage varies, depending on whether it is on a Peasant Farm, European Farm, or Plantation (Development Scheme) Farm level. The extent of the farm problem is in turn affected by the purchasing and marketing system adopted by the territory.

Territories often find it impossible to ignore local customs and local politics, so much so that attempts to put the fruits of scientific research into practice can be very easily foiled. For instance, in a territory which grows large quantities of groundnuts, shelling of the nuts may be done by the women using pestles and mortars, which results in a large percentage of broken nuts and dust. This increases the acidity of the oil and allows insects, such as *Tribolium castaneum*, to breed much faster than they would on whole nuts, and so further increasing the F.F.A. Thus losses from infestation would be curtailed by reducing the breakage of the nuts at shelling. This can be achieved by the use of shelling machines, which can be either the hand type usable by the village women or men, or the large mill type which would take shelling out of the hands of the native. The hand-shelling machines are usually stated to be unsuitable because the women will not work them and it is not a man's job, whereas the installation of large shellers is not deemed desirable because the women are deprived of a paid job and this might result in social difficulties.

Just as fundamental work on the tropical storage problem has been limited by shortage of trained staff, so has applied work. It should also be remembered that the majority of people directly concerned with the storage of valuable foodstuffs, e.g. warehouse-keepers, storage officers, middlemen, etc., have had no training in modern storage methods and techniques.

Indeed, man himself is one of the major problems in food storage. In tropical territories it is much more difficult to assess and to prevent losses in storage due to insects, rodents and micro-organisms than in temperate climates, because of certain human factors.

It is extremely difficult to obtain accurate and reliable figures of quantities of foodstuffs weighed into and out of a depot. A common practice for the storekeeper is to record at intake the accurate weight of the light weight bags and only the required standard weight of overweight bags. Thus a considerable amount of grain is being stored which is not recorded in the official figures. This 'surplus' grain acts as a buffer against which losses due to moisture content change, insect damage, and bad storage are offset and the balance is then sold privately by the storekeeper. Moreover, in certain areas where storage is not properly organized one of the major losses from food storage premises is through pilferage.

In many territories one cannot rely on instructions being efficiently carried out. One must always remember that the local native officers on whom reliance must and should be placed do not always have the background of experience and culture from which we have benefited, and that work will only be carried out as well as the capabilities of the staff concerned will allow. This is especially important on the applied side of the storage problem because it often means that any observations to be made, or control measures to be carried out, must, if they are to be completed with reasonable success, be converted into the simplest form.

Tradition in storage methods and food handling and the difficulty with which man can be made to change his ways in the light of modern research, is an excellent example of man's stubbornness. In some territories maize with the sheath on is dusted with lime or an insecticidal powder during loading into storage cribs. To persuade the farmer to take the sheath off before putting the cob in the crib so that the dust can reach the grains which are often infested before harvest, is a major task.

In recent years politics have begun to play an ever increasing part in making the solution of storage problems more difficult, e.g. the control measures which can be used in storage on the native farm or at the small native mill are limited both in type and efficiency and it is therefore often desirable to set up a marketing system whereby the commodity can be purchased from the farmer as soon after harvest as possible and brought to a central depot where the necessary drying, control and storage facilities exist. Similarly, milling in small native-type mills (e.g. planters' rice mills and hammer mills) is often inefficient, and improvement is only effected by closing down these small mills and replacing them with a few central mills equipped to carry out the milling and storage efficiently. Such improvements, however, can be made impossible by local politics.

SOLVING THE PROBLEM

Although the picture I have painted is dark there are nevertheless rays of light brightening the horizon. I have indicated that solving food storage problems in tropical territories as in temperate areas should be tackled by fundamental, applied and advisory work, e.g.:

(1) Carrying out research on the fundamental aspects of the problem under temperate and tropical conditions.

(2) Investigating problems of an *ad hoc* nature.

(3) Applying available information to existing problems.

(4) Adapting new techniques of control to suit local tropical conditions.

Until 1948 any work carried out in tropical territories was by very harassed government entomologists and had, of necessity, an applied bias. Many examples of this could be quoted, but I have time to mention only a few.

In Africa, M. C. Mossop in Southern Rhodesia as early as 1937 showed the desirability of building large tight stacks of maize to promote self-sterilization by a temperature effect, as well as the importance of *Calandra oryzae* infestations in farm buildings in re-infesting maize growing in nearby fields. He also worked on the tobacco pests, *Ephestia elutella* and *Lasioderma serricorne*, and their control using pyrethrin and DDT sprays respectively. M. S. Oosthuizen in South Africa carried out work on the control of *Calandra oryzae*, *Tribolium* spp., and *Callosobruchus chinensis* attacking stored seed by dusts and fumigants.

In Tanganyika, W. V. Harris and W. F. Jepson did practical work in the construction of bins, methods of handling machinery, and the use of admixing mineral and insecticidal dusts. C. Smee in Nyasaland contributed data on tobacco problems, while in West Africa G. S. Cotterell and F. D. Golding worked on cocoa. In S.E. Asia there is the work on rice storage by H. J. Jack, R. B. Jagoe and H. T. Pagden, and from Fiji R. J. A. W. Lever has published records of their economic storage pests. Stored product work has been carried out in India by H. S. Pruthi and others.

During the past five years more research workers have been specially concerned with storage problems, e.g. in the British territories in Africa prior to 1948 there were seven prominent workers, and since 1948 there have been twenty-one. Considerable progress has been made in tropical territories especially in the application of existing knowledge, and it is also very gratifying to see the recent trends of more emphasis on basic research.

In Australia, S. W. Bailey is working on the effect of concentrations of oxygen and carbon dioxide on *Calandra oryzae*.

Africa, with its diversity of problems, has a number of workers. In 1948, G. S. Cotterell headed a West African Pest Infestation Survey Unit which was financed by the Colonial Office. This survey was concerned with the problems associated with the storage of groundnuts and cocoa, and in 1950 it became the West African Pest Infestation Research Unit financed by the Colonial Office and the Nigerian, Sierra Leone and Gambian Governments. This Unit has built up a considerable amount of scientific data on infestation of groundnuts and cocoa by *Tribolium castaneum* and *Trogoderma granarium* which is helping to reduce storage losses. Control of the work of this Unit, now known as the West African Stored-Products Research Unit, has been taken over by the Nigerian authorities.

Kenya has appointed a Stored-Products entomologist to the Department of Agriculture and their Maize Control Board now employs a Stored-Products Inspector. The work of these two officers is under the control of Kenya's senior entomologist, Dr Le Pelley, and very useful work on the treatment of maize with insecticidal dusts has been reported recently by Kockum (1953). He has shown that a dusting of a 0·04% benzene hexachloride in diatomite dust at a dosage of 1 p.p.m. γ-BHC on cob maize gives protection from *Calandra oryzae* for 12 months under their conditions, and that cob maize can be dusted as heavily as one likes with a BHC dust because after mechanical shelling not more than 0·5–1 p.p.m. remains on the shelled corn.

In Nyasaland, a Colonial Office research worker has been concerned with the maize storage problems since 1951, and work on this commodity will be started in Northern Rhodesia in 1955.

Gold Coast has appointed an entomologist to specialize in stored product problems. A research worker is being sent to Sierra Leone on rice storage and another to Gambia on groundnut problems.

In Southern Rhodesia, extremely useful work with a direct practical bearing has been carried out and published by G. F. Cockbill on the protection of maize, sorghum and beans against insect infestation. He compared the value, at the same cost for insecticide, of a 2½% DDT dust, a commercial 5% BHC dust (containing 0·65% gamma isomer) and a 50% DDT wettable powder, in protecting maize and sorghum stored in bags against *Calandra oryzae* and *Tribolium* spp. and found that the application of 50% DDT wettable powder gave better protection at the same cost than the other treatments and for a longer period of time.

In addition to the valuable background work which is being carried on and expanded in tropical territories, it is extremely encouraging to see colonial territories adopting modern techniques in the applied field. The recent practical developments in colonial territories have been summarized by G. V. B. Herford (Sixth Commonwealth Entomological Conference 1954), but I would like to mention the more important of these.

Pit storage of grain (see Hall & Hyde, 1954), which was originally developed on its present modern lines in the Argentine, is being experimented with by a number of colonial territories including Tanganyika, Nyasaland, Sudan, Nigeria and Gold Coast. Swaine has recorded the rate of build-up of carbon dioxide in Tanganyika's three experimental 120-ton concrete-lined pits, and the success of these experiments in eliminating insect damage has made this territory embark on an 11,000-ton underground storage programme.

More and more territories are putting grain stocks in store in well-constructed conventional silos. Northern Rhodesia have recently opened a 14,200-ton silo of thirty-eight circular concrete bins and are building another; and Uganda have a 12,000-ton capacity silo in thirty-two circular steel bins. Circular steel bin storage for 3400 tons exists in Jamaica. Kenya have been considering silo storage for some considerable time, and it seems likely that they will embark on this in the near future. Trinidad has storage for 1000 tons in circular, welded-steel bins and as these would be ideally suited for hermetic storage if the inlets and outlets were modified, this will be experimented with quite soon. The most efficient method of controlling insect infestation in large concrete or steel bins is by a circulatory fumigation process using the fumigant methyl bromide because by this means even distribution throughout the bulk is ensured. Southern Rhodesia are building a 50,000-ton silo fitted for this method of disinfestation and are contemplating building another of 10,000 tons capacity.

The method of fumigating piles of commodities under gas-proof sheets with methyl bromide has been practised in the United Kingdom since 1946, but it is only now that colonial territories are making use of this method. In Northern Nigeria large quantities of groundnuts (e.g. the 1953 crop was 400,000 tons) have to be stored because of shortage of rolling stock and the method of storing is in pyramids of bagged groundnuts. Since 1949 these pyramids have been fumigated by covering them completely with gas-proof sheets and pumping the methyl bromide through tubing into a chamber excavated at the apex. Many teething troubles such as deterioration of the sheeting under the local conditions (high temperature and ultra-violet light conditions, rough handling) have had to be overcome. However, now that local prejudice against the use of a gas highly toxic to man is being overcome, this method of disinfestation, which makes possible the effective treatment *in situ* of very large quantities of different foodstuffs which previously would have had to be allowed to suffer considerable insect damage, is being adopted by a number of territories. Tanganyika's Department of Grain Storage have now two mobile Fumigation Units which fumigate large stocks of maize, cassava and beans. Each team consists of one European who has been specially trained in the United Kingdom for this work and some six Africans. The Nyasaland Produce Control Board have contracted with a private firm in Nyasaland to carry out this under-sheet fumigation of all their maize stocks, and here again the firm had to have a man specially instructed. In Southern Rhodesia stocks of tobacco have been fumigated in this way. Kenya has carried out small-scale trial fumigation, and is considering adopting this method for the disinfestation of its stocks of maize.

The suitability of the new Ctesiphon-type buildings for the storage of commodities (particularly groundnuts) in tropical countries is being tested in Nigeria. These buildings are built on the catenary arch principle, are cheap, and are relatively gas-tight so that commodities are being stored in warehouse premises which can be easily sealed and fumigated.

THE FUTURE

In many parts of the world more food is being grown to-day than fifteen to twenty years ago, and with improved agricultural practices still more will be grown fifteen to twenty years hence. Thus food storage problems will become more acute and especially in those regions where certain crops fail every three or four years.

A beginning has been made on colonial food storage problems but much remains to be done on the fundamental, applied, and advisory aspects into which I have subdivided the problem.

Much fundamental research work of benefit to tropical territories can be carried out at the Department of Scientific and Industrial Research, Pest Infestation Laboratory, Slough. Basic applied research, however, must be carried out under tropical conditions, and it is suggested that this can only be accomplished by having a group of research workers in a region typical of the wet tropics and one in a region typical of the dry tropics. The advisory aspect is one in which the individual territories are especially interested.

Each territory however feels that it is only by having an expert working on their problems within their boundary that these will be solved. The necessity for pilot schemes to be carried out in the territory with the problem is fundamental to future progress. One must prove a new method of storage or measure of disinfestation in the territory concerned for all there to see before the local authorities are likely to spend money on such a scheme.

As already indicated in this paper, much information requires to be obtained on storage losses resulting from the attacks of insects, fungi and rodents. This can be accomplished only by a one or two years detailed survey carried out in the territory by a stored-product worker with the help of the local department concerned. On this information will rest the extent to which storage methods should be altered and control measures introduced.

This stage will be followed by small pilot experiments or semi-field experiments to determine the effect and importance of local factors. In many territories organizations based on the autonomous-board principle are responsible for purchasing and storing very large quantities of foodstuffs such as maize, worth hundreds of thousands of pounds, yet seldom is it considered worthwhile to employ a scientist who has specialized in food storage. Not even 1% of the total value of the foodstuffs stored is spent on research. In the future these organizations will find, more and more, the need for the employment of a Food Storage specialist. The day is past when such problems can be left to the judgement of the amateur.

With improvements in health and standard of living of the native, serious attention will have to be turned to the problems of native foodstuffs. The small mud storage pot or bamboo crib of each family in which modern control measures cannot easily be carried out will be replaced gradually by village storage. This may perhaps take the form of cheap bulk storage such as is obtained by the new plywood silos which in addition to being cheaper than concrete or brick silos overcome condensation troubles experienced with metal bins.

More properly designed silo storage will be adopted in colonial territories and the future should see developments both of design and construction in hermetic storage above and below ground. If damp grain (i.e. above 13–14% moisture content) can be stored safely in tropical climates in hermetically-sealed structures, drying problems in certain regions of the world will have been overcome.

Improvements in methods of applying insecticides and fumigants will greatly enhance the efficiency of control methods.

Rice, which is the staple food of more than 50% of the world's population, is becoming more and more important and the future should see drastic improvements in rice storage methods. Although some work has been done on rice storage, very little is known, and much more must be learned.

With the interdependence of one country on another and the free trade in foodstuffs, this food storage problem is in some ways akin to the locust problem. Like the locust plague, it must be tackled by every territory, and everybody within the territory must be on the alert. It is imperative that all concerned with food storage in tropical territories should be made 'expert' through attendance at courses, by illustrated pamphlets, exhibitions, etc. The battle is half won if the problem is recognized and the various complications are realized. Future policy will have this as one of its aims.

Just as the ability to store grain in early times allowed civilization to become established by man changing from a nomadic life to a settled existence—so will proper storage techniques linked with sound agricultural practice in the future, open up in tropical territories new economic conditions by eliminating malnutrition and famine.

REFERENCES

COCKBILL, G. F. (1953). Investigations on the control of insect pests of stored grains and pulses. *Bull. Minist. Agric. Lands S. Rhod.* no. 1726, 31 pp. Also *Rhod. agric. J.* **50**, 294–323.

COTTERELL, G. S. & HOWE, R. W. (assisted by JEPSON, W. F.) (1952). Insect infestation of stored food products in Nigeria. Report of a Survey 1948–50, and of control measures adopted. *H.M.S.O. for Colonial Office; Colonial Research. Publ.* no. 12, 40 pp.

HALL, D. W. & HYDE, M. B. (1954). The modern method of hermetic storage. *Trop. Agric., Trin.*, **31**, 149–60.

HOWE, R. W. (1952). Entomological problems of food storage in Northern Nigeria. *Bull. ent. Res.* **43**, 111–44.

KOCKUM, S. (1953). Protection of cob maize stored in cribs. *E. Afr. agric. J.* **19**, 69–73.

SWAINE, G. (1954). Trials on the underground storage of maize in Tanganyika. *E. Afr. agric. J.* **20**, 122–8.

Cann, F. R. (1955). *Ann. appl. Biol.* 42, 98–103

BIOLOGICAL ASPECTS AND ECONOMIC PROBLEMS OF STORED-PRODUCTS ENTOMOLOGY IN TEMPERATE COUNTRIES

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Introductory

The observations made in this paper are based mainly on work done and experience gained in the United Kingdom by the Infestation Control Division, Ministry of Agriculture and Fisheries, the Department of Agriculture for Scotland, the Pest Infestation Laboratory, Department of Scientific and Industrial Research, and the Imperial College of Science and Technology. Similar work is being undertaken in Canada by the Division of Plant Protection, Department of Agriculture, and in the U.S.A. by the Bureau of Entomology and Plant Quarantine, attached to a similar department. Reference should also be made to the work of the Stored Products Working Party of the European Plant Protection Organization, the aims of which are to serve as the European centre for the collection and distribution of information on stored products infestation and methods of control. In its Report (1953) the Working Party passed a resolution to be transmitted to European Governments:

'To examine critically the measures taken within their territories for the prevention of losses to stored food caused by the depredation of insects and other pests: to compare these measures with those in force in other countries in Europe in which knowledge is available and determine whether it is possible to improve the existing inspection and control organization or, if not already in existence, to create one. In view of the necessity for facilitating and not hindering international trade the Working Party recommends that the co-operation of trade interests be sought in each country in devising standards and in other relevant matters.'

The term 'temperate countries' is used here in a wide sense and is intended to apply to Europe, Russia, Japan, Canada, Northern U.S.A., Argentina, New Zealand and Southern Australia.

Biological aspects

Insects and mites infesting stored foodstuffs may be divided into two main groups. The first can be called the Temperate Group and comprises those pests which can live in unheated stores in temperate countries without special protection and which have become endemic pests. Examples are the beetles *Calandra granaria* L., *Oryzaephilus surinamensis* L., *Ptinus tectus* Boiel, and *Laemophloeus ferrugineus* mite, Steph.; the moths *Ephestia elutella* Hubn., and *E. kuhniella* Zell.; and the flour

Tyroglyphus farinae L. These species, with the exception of *Tyroglyphus farinae*, are generally not active throughout the year but survive the winter either in a quiescent state due to the low temperature or in a condition of diapause. They may, of course, remain active when aided by warmth conserved by a commodity, particularly grain, or by heat generated by large infestations.

The ability of these, and other insects, to survive winter conditions in Britain has been recently investigated by Solomon & Adamson (1955), and I am only proposing to remark on a few of the species referred to.

The biology of the spider beetle, *Ptinus tectus*, one of the species most resistant to winter temperatures, has been studied in the laboratory by Howe & Burges (1953). This insect is a widespread warehouse pest in temperate countries, particularly in Britain, where it thrives under cool conditions. The minimum temperature at which complete development takes place is probably between 5 and 10° C.

Laemophloeus ferrugineus over-winters in Canada without difficulty and certainly withstands warehouse temperatures in Britain. Together with *Calandra granaria* and *Oryzaephilus surinamensis*, this species occurs in farm-stored grain in the United Kingdom and induces heating.

Ephestia elutella, another important pest of a wide range of stored products, is probably almost equally resistant to cold and survives the winter in the larval stage in a state of diapause. This insect is a good example of the ability of temperate insects to increase quickly in summer. Huge populations in warehouses may develop from cocoa beans, grain, dried fruit, nuts, tobacco, etc. Richards & Waloff (1946) record that on bulk grain under warehouse conditions in this country there is only one generation a year at temperatures ranging between 15 and 20° C. during the breeding season. On the other hand, at rather higher temperatures in Virginia, U.S.A., Tenhet & Bare (1951) claim three complete generations in certain years, the food material being flue-cured tobacco leaf.

The capacity of these temperate insects for rapid breeding and increase during the warmer months could, apart from other control measures, be counteracted by cool storage for foodstuffs such as nuts, dried fruit and cocoa beans. As opposed to the provision of refrigerated storage space for perishable commodities such as meat, butter, etc., some warehouse-keepers have been aware for some time of the possibilities of cool storage as a means of controlling insects and mites in non-perishable but infestible commodities. For example, just after the last war more than 10,000 tons of shelled almonds were in store in sacks in London warehouses; the attraction of these nuts to the moths *Ephestia elutella* (already resident in many of the warehouses) and *Plodia interpunctella* Hubn. was very marked and the populations of these pests, particularly *Ephestia elutella*, grew to large proportions. In a few of the warehouses, however, the almonds had been put into stowages where the temperature remained within a range of 40–50° F. (5–10° C.). Moths were recorded in these warehouses and breeding probably took place at a very slow rate, but the spectacular migrations of caterpillars seen in other warehouses were notably absent.

The second group of insects can be subdivided into two—those which are being constantly introduced on produce from other temperate countries, for example, *Calandra granaria* in grain from Argentina and Australia, and which serve to reinforce the resident temperate insects, and those arriving from tropical countries.

Among insects introduced into temperate zones from tropical countries many will die because of an insufficiently high temperature for summer breeding, e.g. *Araecerus fasciculatus* Deg. and *Necrobia rufipes* Deg., or more commonly by the insects being killed by winter temperatures, e.g. *Tribolium castaneum* Herbst., *Lasioderma serricorne* F. and *Corcyra cephalonica* Saint. Conditions may, however, be modified in temperate countries and become suitable for the breeding of tropical insects. For example, with artificial heating Pharaoh's ant (*Monomorium pharaonis* L.) and the Argentine ant (*Iridomyrmex humilis* Mayr.) can breed in buildings. The former particularly is well established in bakeries, hospitals, restaurants, etc., where artificial heat is constantly present. The same conditions also encourage the breeding in maltings in this country of *Trogoderma granarium* Everts., a beetle which was brought into Britain from India in grain during the First World War.

Apart from artificial heating, the insulating effect of commodities in bulk or in bags in stacks can help insects such as *Calandra oryzae* L., *Rhizopertha dominica* Fab. and *Ephestia cautella* to survive the winter in this country in unheated warehouses.

ECONOMIC PROBLEMS

The economic problems associated with stored-products pests are numerous and often complicated, covering a wide field of damage and potential loss to many industries. Freeman (1952) has analysed and classified the various types of damage and loss. The most direct type of loss results from actual reduction in weight of the commodity due to insect feeding. Grain and other foodstuffs can suffer loss in dry weight in this way, though—as often occurs in the United Kingdom—such losses may be masked in practice by an increase in moisture content of the commodity due to absorption of water vapour from the air during storage. Loss in weight of a commodity may lead simply to a corresponding and direct financial loss, but between this and the most indirect type, involving loss of trade and commercial prestige far beyond the actual insect damage done, there are types of damage which can produce a combination of direct and indirect loss. Thus, the reduction of the nutritional value of food caused, for instance, by the feeding of mites or *Ephestia elutella* larvae upon the germ of wheat, may be greater than the actual loss in weight.

While direct loss due to insects and mites is generally more pronounced in tropical countries, it is the more indirect type occurring in temperate zones with which I now want to deal.

Attention to the importance of such losses has been drawn by Munro (1929), Herford (1952) and others, who have emphasized how these can be out of all proportion to the value of the actual material consumed or contaminated. Losses of this type may occur at any stage in a commodity's history from the raw material to the finished article.

To give examples, dried yeast in sacks in a warehouse in the north of England became so heavily infested with spider beetles that before delivery the commodity had to be re-bagged with heavy labour costs because of the severe insect damage to the sacks. Again, a large-scale emergence of *Calandra oryzae* from maize in a London warehouse rendered not only the neighbouring stowages unfit for other goods until extensive disinfestation measures had been taken but seriously contaminated a margarine packing depot beneath.

But it is not only the heavier infestations of raw materials which cause indirect loss. The older types of warehouses, mills and other food factories built of brick and timber are more liable to give rise to trading losses due to resident insect and mite pests than modern concrete structures with relatively smooth internal surfaces which do not lend themselves so readily to persistent infestation. In old buildings a high standard of cleanliness is more difficult to maintain and insects and mites can find abundant harbourage and food in the numerous deep crevices amongst the main structural timbers, between floor boards and behind skirting fillets. In spite of attention to hygiene and chemical control, Ptinid beetles, *Ephestia* moths or mites, for example, may emerge from such places and infest or contaminate goods present. The presence of these insects on the goods may cause little real damage but their owners may be sufficiently concerned to require compensation from the warehouse-keeper and even withdraw their custom.

Cross-infestation to materials upon which storage pests do not feed may also have important reactions. For example, *Tribolium castaneum* and *Ephestia cautella* have transferred themselves from groundnuts to chests of tea during shipment, and *E. elutella* larvae have migrated from cocoa beans to empty toffee tins stored in the same warehouse and delivered later to a sweet factory where the infestation was discovered. Cases such as this may involve the custodian of the goods, whether these are in transit or in warehouse, in claims and financial loss.

Trading losses, however, are usually more severe when infestation occurs after manufacture, particularly in the case of branded goods. Since the rationing of foodstuffs during the last war, an increased number of manufacturers has given close attention to the problem of insect and mite infestation in factories. The importance has been learnt of segregating raw materials from finished products and of the need for the strict rotation of stocks. Manufacturers have also learnt the value of obtaining special instruction in insect control for members of their factory staff—particularly in the high standards of cleanliness required. This vigilance must reduce the chances of goods leaving the factory infested and the serious loss of custom and prestige which may result.

From experience, however, many makers of chocolate, malt foods, soup and pudding powders realize that it is of equal importance to protect their wares from insects which may live on the premises of wholesale and retail firms. For example, both *Ptinus tectus* and the Anobiid beetle, *Stegobium paniceum* L. are able to bore through such materials as paper, cardboard and Cellophane. There is also evidence that a very complete seal is necessary for cardboard and paper containers, and even tins, to prevent ingress of first instar larvae of *E. elutella*, an insect of considerable economic importance to the confectionery trade.

A normal rapid turnover of retail foodstuffs in a well-managed shop may give the manufacturers grounds for assuming that any infestation acquired by quickly consumed goods, such as chocolate, will not have reached the stage at which it is detectable by the consumer. A sudden lag in sales may, however, alter the situation and allow an infestation to develop to the point when it is noticeable to the customer.

Apart from the home market, national as well as commercial prestige may be harmed if proprietary goods are exported in an infested condition. These include biscuits, cakes, pudding and soup powders, cigarettes, etc. Moreover, manufacturers in the United Kingdom have not only to ensure that their products are received abroad free from living insects or mites but when competing for markets in the U.S.A. they must rigidly guard against contamination by insect fragments and frass, together with rodent hairs and droppings, in order to comply with the high standards of food purity now demanded by the U.S. Food and Drug Administration.

CONCLUSIONS

While further research will continue to throw light on the biological aspects of stored-products entomology, the greatest need is for the proper application of the large amount of knowledge already available. This need is apparent in all branches of the food industry but particularly requires concerted action in certain branches of the manufacturing, wholesale and retail trades to check cross-infestation which is occurring in branded foods stored together before reaching the customer.

In the United Kingdom the tendency in commerce to ignore or conceal infestation is still prevalent, but the demand for advice and a realization of the basic habits of pests in relation to industrial practices is slowly increasing. This is due partly to the demand for cleaner food and the consequent threat of lost markets; partly to wider publicity on pests and their control—including the more regular and valuable contacts between applied biologists and all branches of the food industry—and also to the statutory powers provided by legislation in the form of the Food and Drugs Act, and the Prevention of Damage by Pests Act, 1949.

I am indebted to Dr J. A. Freeman, who suggested the theme and provided the basic ideas for the composition of this paper.

REFERENCES

European Plant Protection Organization (1953). The protection of foodstuffs in store. *Report of the Stored Products Working Party*. Paris.

Freeman, J. A. (1952). Damage and loss to stored products from attack by insects and mites. *Trans. 9th int. Congr. Ent.*

Herford, G. V. B. (1952). The infestation of stored foodstuffs by insects. *J. Sci. Fd Agric.* **1**, 1–11.

Howe, R. W. & Burges, H. D. (1953). Studies on beetles of the family Ptinidae. IX. A laboratory study of the biology of *Ptinus tectus* Boield. *Bull. ent. Res.* **44**, 461–516.

Munro, J. W. (1929). *Insects and industry*. London: Ernest Benn.

Richards, O. W. & Waloff, N. (1946). The study of a population of *Ephestia elutella* Hubn. (Lep. Phycitidae) living on bulk grain. *Trans. R. ent. Soc. Lond.* **97**, 253–98.

Solomon, M. E. & Adamson, Betty E. (1955). The powers of survival of storage and domestic pests under winter conditions in Britain (in the Press).

Tenhet, J. N. & Bare, C. O. (1951). Control of insects in stored and manufactured tobacco. *Circ. U.S. Dep. Agric.* no. 869.

Parkin, E. A. (1955). *Ann. appl. Biol.* **42**, 104–111

PROGRESS IN THE CONTROL OF INSECTS INFESTING STORED FOODSTUFFS

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I have been invited to review briefly progress in the control of insects infesting stored products, with special reference to the United Kingdom and the last fifty years. This period may be divided into two distinct halves. In the first, the subject of stored-product entomology was scarcely recognized, and little real progress was made in the discovery and application of control measures. In the second, not only has the subject attained an importance which, against the background of possible world food shortages, places it high in the ranks of applied science, but the few workers so far engaged in this specialized field have managed to provide practical and economic solutions to a number of the problems of control which have arisen.

The past: 1900–25

For the first quarter of this century biological knowledge of the conditions favouring the increase and spread of infestations was largely lacking and means for control scarcely existed. It is true that carbon disulphide, hydrogen cyanide, chlorpicrin, and methyl formate were often recommended for fumigation of infested produce, but they seem to have been seldom employed and then mostly in small chambers with a capacity of a few cubic feet.

During the First World War the problem of grain storage became acute in the United Kingdom and in Australia, and was investigated in this country by the Grain Pests (War) Committee of the Royal Society. Their reports disclose investigations into control by the use of hermetic storage, reduction of moisture content, fumigation with formaldehyde, sulphur dioxide, ammonia, ether, alcohol and ozone; the use of heat sterilization in Australia was also reported on by a special team sent out by the Royal Commission on Wheat Supplies.

Up to 1925, therefore, research into insect control in stored foodstuffs had been undertaken in Great Britain only under pressure of war and had been dropped as soon as the pressure eased. No control measures appear to have been put into operation in the United Kingdom during this period. What had been learned was basically important but was useless in practice at the stage in which it had to be left.

THE PRESENT: 1926–54

At the beginning of this period four figures appeared on the scene whose influence on stored-product entomology has been immense: Zacher in Germany, Back and Cotton in the United States, and Munro in Great Britain. In 1927 Munro joined the staff of the Department of Entomology and Applied Zoology at the Imperial College of Science and Technology. He immediately impressed on his students the coming importance of stored-product entomology and his foresight and faith in the eventual wider recognition which must come to this subject has been the ultimate origin of all the subsequent developments in this country. As a result of his influence, the Pest Infestation Laboratory was set up in the Department of Scientific and Industrial Research in 1940 as a research station. In 1942, it provided staff towards the formation of the Infestation Control Division in the Ministry of Food (now in the Ministry of Agriculture and Fisheries and the Department of Agriculture for Scotland) as an inspectorial and advisory body. In the United Kingdom we can now consider ourselves second to none in our organization, enthusiasm and achievements.

During the past twenty-five years, impressive additions to our knowledge of the biology and distribution of the insects and mites concerned, of the risks of cross-infestation during storage and transport, and of the conditions of storage and transport in many parts of the world, especially in the colonial territories, have gone hand in hand with equally great advances in methods of prevention and control of infestation. I need hardly remind you that control measures can be properly recommended or applied only with a good knowledge of the other aspects I have just mentioned, to which I would add knowledge of pertinent trade practices.

Hygiene

The first line of progress that I would like to record is the realization of the immense importance of hygiene. Cleanliness and order in the store reduce insect populations, and hence the risk of damage; moreover, they make control measures, when required, easier to apply and more effective. Although it can be said that the scientist now knows and stresses the various aspects of hygienic practices, we are unfortunately trying all too often to change human nature in our attempts to get these practices adopted: some people are just naturally untidy and any enforced change of habit tends to be short-lived.

Storage methods

A study of the generation and spread of hot-spots in bagged grain, most of which are provoked by insect infestation, has led to recommendations in hot, dry climates that bag stacks should be as large and as tight as possible to encourage internal heating and consequent sterilization. A procedure that would invite disaster in this country can thus be used to good effect in some tropical areas as a method of partial control which frees the centre bags from insect infestation and leaves only the peripheral bags to be treated with contact insecticides. This recommendation rests on knowledge of the movement of heat and moisture through grain, and of the physical condition of the grain when put into store, allied to data on the local climate. Similar knowledge, but also embracing the respiration rates of grain and insects, underlies the recent large-scale trials in Africa and elsewhere of the auto-sterilization of insect-infested grain during long-term storage in specially constructed pits in the soil.

Heat

Control by heat has long attracted attention but, in spite of continued investigations embracing the new methods of heating products by infra-red or high-frequency electrical radiations, it has never quite become a practical proposition. This is due partly to cost and partly to the small differential between the temperatures and exposure periods required to kill the insects and those which damage the product.

Mechanical control

An interesting form of mechanical control of infestation, embodied in the entoleter, has become popular in factories packing powdered products. Immediately before entering the pack, the product passes through a machine in which it is flung with considerable centrifugal force against a revolving set of steel pillars. If correctly used, this machine can ensure that the packaged product will contain no living stages of insects or mites.

Fumigants

Turning now to chemicals for the treatment of stored foodstuffs, I will deal first with the fumigants. It is very definitely only in the last twenty-five years, and particularly in this country, that we have started studying the process of fumigation scientifically: (*a*) by determining the concentrations and periods of exposure needed to ensure the death of all stages of a wide range of species of insects and mites at temperatures likely to be encountered in practice; (*b*) by using special methods of gas sampling to investigate the rate of penetration of gases into different types of goods packed or stacked in different ways; and (*c*) by assessing the quantity and importance of chemical residues from the treatment with respect to possible deleterious effects on the product or toxicity to the consumer. Twenty-five years ago the first detailed studies were started of the behaviour of hydrogen cyanide and ethylene oxide under the conditions of practical fumigation. These studies have been steadily pursued and extended to methyl bromide and the chlorinated hydrocarbons so that, in conjunction with the results of laboratory studies of toxicity to insects and of the importance of residues in foodstuffs, workers can build up a picture of the probable distribution of the gas, insecticidal effectiveness, and likelihood of contamination under most practical conditions. Moreover, piping and pumping systems have been improved, 'cocoon' plastics have been added to the methods for gas-tight sealing, and practical ways have been found of fumigating parcels of infested goods, from a few tons to several hundred tons in size, under gas-proof sheets without need to seal a stowage or evacuate other than the one in which the treatment is in progress. Techniques of vacuum fumigation in suitable chambers are now being improved and, as a last remark on fumigation, I would mention the advances in design and operation of installations for circulating fumigants through silo bins full of grain, a method of fumigation so enthusiastically adopted in some countries and so neglected in our own.

Contact insecticides

Pyrethrum. Turning now to contact insecticides, we find that they were not used in warehouses, etc. until pyrethrum was introduced in the early 1930's for control of moths and caterpillars infesting dried fruit. This specialized use of non-volatile oil solutions of pyrethrum as fogs and later as films deposited on the fruit boxes remained the only control measure with contact insecticides in practical use until 1940. The change in storage conditions consequent upon the start of the Second World War encouraged the growth of insect infestations, and lack of alternatives forced the adoption of pyrethrum sprays for the control of insects, especially the many species of beetles that attacked other products than dried fruit, the most important by far being grain. Spraying the surface of bulk grain was effective in keeping down the number of moths but was less successful against the beetles. It was soon shown that oil films of this and other insecticides deposited on such common absorbent surfaces as brick, limewash, cement, or concrete had an effective toxic life of at most a few hours. However, it was found that, under suitable circumstances, walls, etc., could be pretreated before spraying with a solution of size or gelatin such as would interpose a non-absorptive layer between surface and oily film, resulting in a relatively enormous increase in the effective toxic life of the film. The value of pretreatment still awaits proper appreciation.

Inert dusts. Because of the war-time scarcity of pyrethrum, alternative means of control of grain insects were sought and, following a lead given in pre-war Germany, the possibilities of inert mineral dusts were investigated. From 1940 onwards a diverse selection of finely powdered minerals and industrial wastes was tried in laboratory sorting tests in this country in the hope that some cheap, available substance, preferably a waste product, would be insecticidally effective. Unfortunately, the most available materials tended to be the least effective or had some toxic hazard for man and, although full-scale trials of materials finally attaining the short list showed promise, the inert mineral dusts just failed to find application in this country. However, they were used with some success in Australia and other parts of the world, and one based on ground rock phosphate is in common and current use in the dry regions of the Near and Middle East.

DDT. Late in 1942, DDT reached this country and the U.S.A. As soon as the preliminary work to assess its value in the control of lice, flies, and mosquitoes was well in hand, attention was turned to determining, among other things, the value of this exciting new insecticide in the field of stored-product entomology. Early work showed that there were difficulties in using it freely in food-storage premises because of the toxicological risks to man and animals consuming contaminated food. In addition to considering how best to apply the insecticide to ensure that the insects come into adequate contact with it, investigation has, therefore, to be made of the types of formulation and methods of application most likely to cause minimal transfer of the insecticide to the commodity. Chemists have been set the difficult task of finding precise methods of determination of the chemical in the presence of food extractives, methods sensitive to one part per million or less. This level of sensitivity has, in turn, been based on the painstaking work of toxicologists investigating the chronic toxicity to animals of small quantities of insecticides like DDT in the diet. The use of DDT in our field of work has been severely curtailed by the tolerance limit of 7 p.p.m. which has been accepted in this and some other countries, as well as by its slow toxic action and the relatively high natural resistance of some important pest species. Nevertheless, there are a few species of stored-product insects which can be controlled by doses close to the tolerance limit for DDT. Much information has now been gathered about the advantages and disadvantages of DDT for the control of insects infesting stored foodstuffs and I think that interest in this chemical will increase somewhat again in the future. It is intriguing to note in passing that several years of intensive efforts by chemists in synthesizing homologues and analogues of DDT have not yet produced a more useful compound. Similar efforts by insect physiologists have also failed so far to disclose in full its mode of action on insects.

γ-BHC. Scarcely had work started with the one 'new' insecticide DDT than attention had also to be given to another, 666, the toxic component of which is now known as γ-BHC. Here was another synthetic chlorinated organic compound with many general similarities to DDT but faster acting, more toxic to insects and mammals and, because of its volatility, highly toxic in the vapour phase but less persistent. Unlike the pyrethrins and DDT it was found to possess a marked acaricidal effect. The high propensity of crude BHC to taint foodstuffs retarded the extension of its use in food warehouses at first. However, the fairly recent development of insecticides formulated with lindane (99% or more γ-BHC) has overcome this disadvantage and γ-BHC is now being used more and more for the control of stored-product insects, but a limit may be set by its volatility. In certain circumstances the slow permeation of the vapour throughout closely piled goods can be made to perform a function akin to fumigation. The very high toxicity of the vapour to insects has, incidentally, made the interpretation of results of laboratory tests with this and similarly volatile insecticides very difficult, as it is well-nigh impossible to parallel in the laboratory the conditions of exposure and variable ventilation which will occur in practice. A tolerance limit of 2·5 p.p.m. of γ-BHC has now been fixed and at this level of dosage one or two more species of stored-product insects can be controlled than with the corresponding limiting dose of DDT.

The immediate position

At the moment, then, we can consider ourselves very well placed in the struggle against insect infestation if our basis for comparison is the immediate pre-war period, say fifteen years ago. We are well armed with biological and ecological knowledge of the main pests with which we have to contend, and we have more knowledge of methods of warehouse handling and hygiene which can be utilized to minimize infestation. We can choose the most suitable formulation of our insecticide (DDT, BHC, or pyrethrins with or without synergists) from among dusts, pastes, wettable powders, solutions, emulsions, lacquers, and so forth, and apply it by a varied array of dusting, spraying, fog or smoke-generating, and vapour-dispensing applicators. Nevertheless, problems crowd upon us which seem incapable of practical solution in our present circumstances.

At this point I would emphasize that we have been working with DDT and BHC for over ten years and we have still by no means fully evaluated these two compounds in the restricted field of stored-product entomology. Yet awaiting detailed appraisal we already have an accumulation of other chemicals such as allethrin, furethrin, aldrin, dieldrin, endrin, isodrin, chlordane, heptachlor, and so on, and at any time organo-phosphorus compounds with a lower mammalian toxicity or totally new insecticides may be prepared by the chemists. Most of the newer compounds, however, have disadvantages at least as great as those of DDT and BHC. I would add here, in parenthesis, that knowledge of acaricides for use against mite infestations of stored products is meagre and a study of this subject may yield valuable results.

Where there is any question of hazard to the health of man or animals, the policy must obviously be 'Proceed with caution', and I think that this is achieved in this country by the balance between the eagerness of the insecticide industry to put new products into use and the scientific caution of the research worker. Nevertheless, criticism is often levelled at the scientist for the apparent slowness of research without bearing in mind the wide gap between existing knowledge and its full utilization.

THE FUTURE

Having dealt with the past and the present, what of the future?

In spite of the tremendous improvement recently in our knowledge of stored-product insect control, those who have to give practical advice will be only too keenly aware of the number of problems which still remain unsolved and of the huge amount of information which still needs to be gained. I have already mentioned the mass of background work which needs to be done to evaluate properly all the candidate insecticides now awaiting full examination and, even with the established insecticides like DDT and BHC, we still want more information on their persistence under varied warehouse conditions, their transfer to goods in store, and their fate during subsequent handling and processing. Particularly do we need data on these points in relation to tropical conditions of storage. The trial of new synthetic compounds as insecticides will obviously continue and, although no one can forecast when success will be attained, any day may see the birth of a compound which could completely change the present picture of stored-product insect control if it possessed a combination of cheapness, fast action, high toxicity to insects difficult to control with existing materials, low toxicity to mammals, and freedom from taint.

Even if this discovery is made we must continue to press for better construction of silos, warehouses, go-downs, mills, etc. with a view to easy detection of infestation and application of control measures if they should become necessary. Managers must be made more aware of their responsibilities for insect infestation and of the benefits of early detection and treatment; and encouraged to make full use of the methods of control already available. In particular, I feel that better methods of disposal of infested sweepings and screenings must be got into practice. Indeed we need to impress upon those responsible the adoption of every method of hygiene and mechanical protection to enable the use of insecticides to be avoided, although I am regretfully convinced that they will never cease to be necessary.

More detailed scientific measurement is required of the numbers and distribution of insect populations in goods and premises, the effect on the population of the application of insecticidal measures, and the rate of recovery of infestations from small numbers of survivors.

Improvements in methods for the chemical determination and biological evaluation of insecticides must be sought and accumulation of data on the resistance to insecticides of a wide variety of insect species and stages must continue. Perhaps the greatest need at the moment is for more work in toxicological laboratories on the hazards of chronic poisoning from those compounds standing on the brink of extensive trials. The reports of the Delaney Committee in the U.S.A. and the Zuckerman Working Party in Great Britain point the need to know as much as possible about the toxicology of insecticides which may find their way in small quantities into foodstuffs. The setting of tolerance limits in this country for DDT and γ-BHC, based on long-term animal-feeding tests, has proved of the utmost value in making recommendations for treatment, although such limits have no legal status. The limits must be used sensibly however, and with due regard to all the pertinent circumstances. If ill-founded fear is allowed to displace respect for the mammalian toxicity of these compounds, the conditions governing their use may be made so stringent that the insecticides are not usable in doses sufficient to kill any insects.

I do not confidently anticipate the discovery of a new insecticide which will be the panacea to prevent or cure all types of insect infestations in stored products, but we can look forward to a wider choice of suitable compounds. The practical problems presented are so varied that knowledge must be built up of as wide a variety of control measures as possible so that among them is likely to be found one, or a combination, that can be used in any given set of circumstances. I believe that the biggest planned gain in practical control will now come from focusing attention on particular insect species in particular products. This will lead automatically to study of the biology and behaviour of each species in association with the product under commercial conditions of handling and storing and to the trial of insecticides using such formulations and methods of application as will best fit in with trade practices, as will keep contamination of the product within acceptable limits, and as will hit the insect in its most vulnerable phases. This means that generalization of instructions for control is not likely to become possible, and only the specialist will be able to prescribe the proper cure. However, this could usefully lead to an increase in the numbers of technical consultants and of servicing firms with a special interest in the field of stored-product entomology.

We must be on the watch for the development of resistant strains of stored-product insects. None of real significance has yet appeared and some workers consider that they are not likely to do so, but I think that some species will eventually be able to find suitable conditions in warehouses, etc., to evoke any potentiality towards high resistance. Let us hope that no such potentiality exists.

In conclusion, I should like to stress the need for encouraging greater co-operation between importing and exporting countries to ensure that all reasonable steps are taken to keep infestation to a minimum in stored foodstuffs entering into international trade. Here, unfortunately, progressive entomology comes up against the traditional and reactionary nature of some commercial practices. It is sad to record that, in spite of the great amount of easily available knowledge of the biology and control of the insects and mites concerned, infestation in some commodities is still regarded in trade circles as 'inherent vice' and therefore, presumably beyond prevention or control. We cannot, therefore, rest content with scientific advances but must patiently continue to try to educate all concerned to realize that a pennyworth of control applied early may save a pound's worth of loss later.

Plant viruses and virus diseases

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PAST AND PRESENT TRENDS IN PLANT VIRUS RESEARCH

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In presenting to you this brief survey of plant virus research I propose to recall some of the outstanding discoveries in the more remote past and then to pass rapidly over what I may perhaps refer to as the middle or dark ages of plant virus research. We come then to the nineteen-thirties when the more modern scientific attack upon the plant virus problem began. It was really about this time that virus research as a whole started to overflow into many other disciplines. This brought in the biochemist, the physicist, the serologist and other workers in quite remote fields, and it was from this concerted attack that much of our fundamental knowledge of plant viruses has accrued.

Mayer, in 1882, was one of the first workers on the classical tobacco mosaic disease and it was he who showed it to be infectious and coined the phrase 'mosaic disease' which is now universally applied to virus diseases with mottling symptoms. The first scientific demonstration of the existence of a virus was, of course, made by Iwanowsky in 1892, who proved that the sap of mosaic-diseased tobacco plants was capable of inducing the disease in healthy tobacco plants after passage of a bacteria-proof filter candle. Then in 1906 Baur showed that the so-called variegation of *Abutilon* spp. could be transmitted by graft and called it an 'infectious variegation'. In 1912 Allard conveyed tobacco-mosaic virus to potato, and in 1916 Quanjer, Lek & Oortwyn Botjes in Holland discovered the infectious nature of potato leaf roll. This last discovery was important in that it gave the death-blow to the theories of 'senile decay' and later showed that the degeneration of potatoes was due solely to the spread of viruses through the crop. For some years after this much of the energy of the small group of plant virus workers was directed mainly to the study of symptoms and the discovery of new virus diseases. Some interesting viruses were brought to light during this period, among which may be mentioned those of tomato bushy stunt and tobacco necrosis (Smith, 1935; Smith & Bald, 1935). In 1928 Holmes showed that there existed a relationship between the concentration of tobacco-mosaic virus and the number of local lesions which develop on the inoculated leaves of *Nicotiana glutinosa*. This discovery has made possible the quantitative study of plant viruses and allows for comparative estimates of virus concentration. This technique has been extended to a number of other viruses, and is of the greatest use in many procedures with plant viruses.

Purdy Beale's discovery in 1928 that tobacco-mosaic virus was a powerful antigen has been the foundation of an important branch of plant virus research. She found that the virus when inoculated into rabbits gave rise to antibodies specific for that virus. This has enabled us to discover relationships between viruses which would not otherwise have been suspected, such as that between tobacco-mosaic virus and cucumber viruses 3 and 4 (Bawden & Pirie, 1937).

The question of latent viruses is one of great interest and importance, not only in plant viruses but in viruses as a whole, since they are known to occur in many different types of organisms. The description by Salaman & Le Pelley in 1930 of the latent virus, paracrinkle, in potatoes of the variety King Edward, was about the first of the truly latent plant viruses to be discovered. In speaking of paracrinkle virus as truly latent one should perhaps make the reservation that as no one has yet seen a King Edward potato plant free of this virus it is possible that there may be characteristics which are due to its presence. Much speculation has centred upon the paracrinkle virus, and the question of how it entered the original seedling has never been answered. The fact that it has apparently no means of natural spread is another interesting point. By showing that paracrinkle virus can be spread by mechanical methods, Bawden, Kassanis & Nixon (1950) have removed some, but not all, of the mystery surrounding it.

What is perhaps an even more interesting case is the latent virus of sugar beet (Smith, 1951, 1952). At certain times of the year this virus occurs in an extremely high percentage of sugar beets and mangolds, especially in the late summer, and then disappears again. It does not seem to be seed or soil-borne and no insect or other vector has been found. Its presence in the sugar beets and mangolds is not revealed by any symptoms whatsoever, but it can be detected by sap-inoculation to cowpea, *Vigna sinensis*, on which it gives rise to local lesions. Further research may throw some light on its method of spread, if it does spread. Alternatively, it may be always present in the plants in quantities undetectable by present methods, and only multiplies up to measurable amounts under certain environmental conditions. This theory, of course, presupposes seed-transmission of the virus, which we have not yet been able to prove.

Kassanis (1954) has made the interesting discovery that many potato varieties, including King Edward, are symptomless carriers of a latent virus from carnations. It is transmissible, also, to other plants in which it produces no symptoms and, in fact, the only plant in which it appears to have caused any symptoms is the sugar beet. The virus, however, can be transmitted by the aphid *Myzus persicae*. This ubiquitous insect, which is the vector of between twenty and thirty plant viruses in different parts of the world, first came into prominence when it was shown to be the chief vector of the potato leaf-roll virus (Smith, 1929). The relationship between plant viruses and their insect vectors has been under investigation for a number of years and is still incompletely understood. In 1932 Storey showed that there existed two races of leafhoppers morphologically indistinguishable, one of which could, and the other could not, transmit the virus of streak disease of maize. Storey called these two races 'active' and 'inactive' respectively. The reason for this appeared to lie in some difference in permeability of the gut wall, because a puncture made with a fine needle in the wall of the alimentary canal of the inactive race enabled them temporarily to become vectors. Since then this same phenomenon has been shown to exist with other leafhopper vectors (Black, 1943). Watson & Roberts, in 1939, defined plant viruses in relationship to their insect vectors as 'persistent' and 'non-persistent', according to the time the insects retained infectivity without again having access to a source of virus. Most, but not all, of the persistent viruses have leafhoppers for vectors, and it is in reference to these that workers long debated the question as to whether the virus multiplied in the insect vector. Three American workers, Kunkel (1937), Black (1950) and Maramorosch (1952) in independent studies spread over a number of years, have demonstrated that some plant viruses do multiply in their insect vectors. Black found that the clover club leaf virus was transmitted from viruliferous females of *Agalliopsis novella* to their progeny through the egg, and he showed that the virus in a single female was capable of being maintained through twenty-one generations of progeny during a period of five years, without access to virus from plants. Black has calculated that if the virus did not multiply it would have undergone a dilution of 10^{-26}. A somewhat similar experiment was carried out earlier by Fukushi (1940) who demonstrated the passage of rice stunt virus to eighty-two leafhoppers in six generations.

In a different type of experiment Maramorosch succeeded in transmitting the aster yellows virus by direct inoculation to the insect through ten serial passages from insect to insect without loss of virus concentration.

These and other experiments have now proved that some at least of the leafhopper-transmitted plant viruses do actually multiply inside their insect vectors. This is an important discovery since it makes a link between the plant and animal viruses, and may even suggest that some of these viruses started as insect viruses and mutated or became attuned to multiplication in plants.

While the great majority of plant viruses are transmitted by sucking insects, the virus of turnip yellow mosaic affords a good example of transmission by biting insects. In nature the vectors are various species of flea beetles, but it has been shown experimentally that any biting insect which regurgitates can act as a vector (Markham & Smith, 1949).

Up to the year 1935, plant virus research had been mainly concentrated upon the diseases and upon the insect vectors, but since that date the focus has been much more on the virus itself. This is largely due to the isolation of the tobacco-mosaic virus by Stanley (1935) who was one of the first to treat the virus more as a chemical substance than an organism and precipitated it by means of ammonium sulphate. A little later the virus was shown by Bawden, Pirie, Bernal & Fankuchen (1936) to be a nucleoprotein, and in 1937 Bawden & Pirie purified and crystallized the virus of tomato bushy stunt. This was the first virus to be crystallized in the form of true 3-dimensional crystals, dodecahedra, as compared with the paracrystals or liquid crystals of tobacco-mosaic virus.

At intervals since then various other plant viruses have been purified and crystallized, such as a tobacco-necrosis virus (Pirie, Smith, Spooner & MacClement, 1938), southern bean mosaic virus (Price, 1946) and turnip yellow mosaic virus (Markham & Smith, 1949), which was the first insect-transmitted virus to be crystallized.

The purification of plant viruses, together with the development of the electron microscope, have now enabled us to see the viruses which for so long have been invisible. It was first suggested in 1933 by Takahashi & Rawlins that the tobacco-mosaic virus particles were rod-shaped. This was because sap from a tobacco-mosaic plant showed the phenomenon of 'anisotrophy of flow' which indicates the presence of rods. When tobacco-mosaic virus was photographed on the electron microscope this suggestion was amply confirmed. Actually the virus particles measure $300 \times 15\,m\mu$.

Quite a number of plant viruses have now been photographed on the electron microscope and their size measured with some accuracy. Some viruses are spherical, or near spherical; these are tomato bushy stunt, turnip yellow mosaic and southern bean mosaic viruses, whilst the viruses with rod-shaped particles which may be mentioned are tobacco-mosaic virus and cucumber viruses 3 and 4. Potato virus X is also rod-shaped but lacks the rigidity of the tobacco mosaic virus. It is hoped, however, to do much more with the electron microscope than measure particle size and shape. By means of the new technique of embedding in plastic and the specially designed microtome it is now possible to cut ultra-thin sections for examination in the electron microscope. By this means one can see the virus particles inside the cell, and the next step will be to follow the multiplication of the virus. This is a subject of which we know very little, although a few hints can perhaps be gathered from contemporary work. The virus of turnip yellow mosaic is a very interesting one from several aspects, and especially because of its existence in two parts, which have been called the top and bottom components (Markham & Smith, 1949). When a purified solution of the virus is centrifuged for 2 hours at 12,000 r.p.m. it separates sharply into these two components. The top component, which is usually about 20% of the whole, contains no nucleic acid and is not infectious. The bottom component, otherwise similar in every respect, does contain nucleic acid and is infectious. This seems to be the first experimental evidence that nucleic acid was concerned with the multiplication of viruses. Markham (1951) made a study of the physical properties of the particles of the two components and came to the conclusion that the nucleic acid was contained in the centre of the bottom component particles whilst those of the top component were hollow. This supposition has since been confirmed by X-ray studies carried out at Wisconsin (Schmidt, Kaesberg & Beeman, 1954). The important question now arises as to the relationship between the top and bottom components. Is the former a pro-virus, an imperfectly synthesized virus or what? Some light has been shed on this problem by Jeener (1954) who used labelled carbon dioxide. At a certain stage in the development of the yellow mosaic disease he introduced the plant into the labelled CO_2. He found that the labelled CO_2 went first into the top component showing that this is an earlier stage in the synthesis of the virus. Markham has suggested, purely as a speculation, that there might be an analogy here with the mechanism of reproduction in bacterial viruses as shown by Hershey & Chase (1952). In other words, the top component particles resemble the 'ghosts' of the bacterial virus particles which have lost their nucleic acid after it has been passed down the 'tail' of the virus particle into the bacterium. Under these circumstances the particles of the top component are the empty shells from which the nucleic acid has emerged to produce two daughter virus particles.

The fact that nucleic acid plays such a vital part in the multiplication of a plant virus has led to the development of chemotherapy using chemicals which attack the nucleic acid. The interesting fact has been demonstrated by Matthews (1954), working with 8-azaguanine, that this substance when sprayed on to the plants inhibits the development of several plant viruses. Furthermore, in the case of tobacco-mosaic virus, it is incorporated into the virus nucleic acid replacing part of the guanine so that particles containing 8-azaguanine are incapable of multiplication. Similarly, Commoner & Mercer (1952) have inhibited the multiplication of tobacco-mosaic virus by means of thiouracil and it has been claimed by Jeener & Rosseels (1953) that this substance also is incorporated in the nucleic acid of tobacco mosaic-virus.

It is impossible in a short review to cover all aspects of plant virus research, but mention should be made of cross-immunization between plant viruses and the interaction between viruses. The discovery was first made by Thung (1931) working with different strains of tobacco-mosaic virus, and later by Salaman (1933) with potato virus X, that like viruses and virus strains would cross-immunize and this has proved a useful tool in the study of virus relationships. Arising, perhaps, out of this discovery has been the study of the interaction between viruses in the same plant. An example of this is the inability of potato virus Y to multiply in plants infected with severe etch virus (Bawden & Kassanis, 1945). There is also the occurrence of the so-called 'carrier viruses'; such a phenomenon is found in the rosette disease of tobacco (Smith, 1946). Here there are two viruses acting in unison to form the rosette disease, the mottle and vein-distorting viruses respectively. When together *in the plant* they are both transmissible by the aphid, *Myzus persicae*, but when separated in different plants only the vein-distorting virus is aphid-borne. The explanation of this phenomenon is at present obscure, but it is probable that other examples of 'carrier' viruses exist, and indeed Clinch, Loughnane & Murphy (1936) have stated that it is necessary for potato virus A to be present in the potato plant to enable the aphid, *Myzus persicae*, to pick up potato virus F (tuber blotch virus). The whole subject of the interaction between plant viruses has recently been ably reviewed by Bennett (1954).

The classification of plant viruses and their nomenclature constitute a controversial problem but one of great practical importance, and its ultimate solution lies very much in the future. The problem has already been tackled by several workers from different angles and, as everyone knows, Dr Holmes has been courageous enough to launch a comprehensive scheme of virus classification upon a troubled virus world. There seem to be two main difficulties in arriving at a stable system of classification of plant viruses. First, there is no one characteristic or property which would serve as the main basis of the scheme, and secondly, we only know a little about a few viruses when we need to know a lot about many. For example, we can now photograph a number of viruses on the electron microscope but morphology is not enough. Who is going to be bold enough to attempt to distinguish tomato bushy stunt virus from that of turnip yellow mosaic from their photographic appearance alone? Again, serological reactions would seem to be an ideal basis for classification but the number of viruses to which that could be applied is very small compared to the total number of plant viruses, which must now number about 250. Here, incidentally, is another problem to be solved, why is it that no antisera can be obtained for so many plant viruses? The main foundation for the present scheme of plant virus classification is symptomatology and that is a treacherous foundation enough. No doubt in the future a sound scheme of classification will be built on all these properties and others as well, morphology, serological relationships, insect vectors, symptomatology, host range, etc., but for the present, as I have already said, we do not know enough, and that seems to be an appropriate sentence with which to end this survey.

REFERENCES

ALLARD, H. A. (1912). *Science*, N.S., **36**, 875–6.
BAUR, E. (1906). *S.B. preuss. Akad. Wiss.* **1**, 11–29.
BAWDEN, F. C. & KASSANIS, B. (1945). *Ann. appl. Biol.* **32**, 52.
BAWDEN, F. C., KASSANIS, B. & NIXON, H. L. (1950). *J. gen. Microbiol.* **4**, 210.
BAWDEN, F. C. & PIRIE, N. W. (1937). *Brit. J. exp. Path.* **18**, 275–91.
BAWDEN, F. C., PIRIE, N. W., BERNAL, J. D. & FANKUCHEN, I. (1936). *Nature, Lond.*, **138**, 1051.
BENNETT, C. W. (1954). In *Advances in virus research*, **1**. New York: Academic Press.
BLACK, L. M. (1943). *Genetics*, **28**, 200.
BLACK, L. M. (1950). *Nature, Lond.*, **166**, 852.
CLINCH, P., LOUGHNANE, J. B. & MURPHY, P. (1936). *Sci. Proc. R. Dublin Soc.* **21**, 431–48.
COMMONER, B. & MERCER, F. L. (1952). *Arch. Biochem. Biophys.* **35**, 278.
FUKUSHI, T. (1940). *J. Fac. Agric. Hokkaido Univ.* **37**, 2, 41.
HERSHEY, A. D. & CHASE, M. (1952). *J. gen. Physiol.* **36**, 39.
HOLMES, F. O. (1928). *Bot. Gaz.* **86**, 66–81.
IWANOWSKY, D. J. (1892). *Bull. Acad. Imp. Sci. Petersburg*, **35**, 67.
JEENER, R. (1954). *Biochim. biophys. Acta*, **13**, 161.
JEENER, R. & ROSSEELS, J. (1953). *Biochim. biophys. Acta*, **11**, 438.
KASSANIS, B. (1954). *Nature, Lond.*, **173**, 1097.
KUNKEL, L. O. (1937). *Amer. J. Bot.* **24**, 316.
MARAMOROSCH, K. (1952). *Phytopathology*, **42**, 59.

Markham, R. (1951). *Disc. Faraday Soc.* **11**, 221.
Markham, R. & Smith, Kenneth M. (1949). *Parasitology*, **39**, 330–42.
Matthews, R. E. F. (1954). *J. gen. Microbiol.* **10**, 521.
Mayer, G. E. (1882). *Woorloopie Meded. Landbou. Tidschr.* pp. 359–64.
Pirie, N. W., Smith, K. M., Spooner, E. T. C. & MacClement, W. D. (1938). *Parasitology*, **30**, 543.
Price, W. C. (1946). *Amer. J. Bot.* **33**, 45–54.
Purdy (Beale), H. A. (1928). *Proc. Soc. exp. Biol., N.Y.*, **25**, 702–3.
Quanjer, H. M., Lek, A. H. & Oortwyn Botjes, J. (1916). *Meded. LandbHoogesch., Wageningen*, **10**, 1.
Salaman, R. N. (1933). *Nature, Lond.*, **131**, 468.
Salaman, R. N. & Le Pelley, R. H. (1930). *Proc. Roy. Soc.* B, **106**, 50–83.
Schmidt, P., Kaesberg, P. & Beeman, W. W. (1954). *Biochim. biophys. Acta*, **14**, 1.
Smith, Kenneth M. (1929). *Ann. appl. Biol.* **16**, 209–28.
Smith, Kenneth M. (1935). *Ann. appl. Biol.* **22**, 731–41.
Smith, Kenneth M. (1946). *Parasitology*, **37**, 21–4.
Smith, Kenneth M. (1951). *Nature, Lond.*, **167**, 1061.
Smith, Kenneth M. (1952). *Biol. Rev.* **27**, 347.
Smith, Kenneth M. & Bald, J. G. (1935). *Parasitology*, **27**, 231–45.
Stanley, W. M. (1935). *Science*, N.S., **81**, 644–5.
Storey, H. H. (1932). *Proc. Roy. Soc.* B, **112**, 46–60.
Takahashi, W. N. & Rawlins, T. E. (1933). *Science*, **77**, 26–7.
Thung, T. H. (1931). *Handelingen 6de Nedesl. Inde. Naturwetensch. Congr.* pp. 450–63.
Watson, M. A. & Roberts, F. M. (1939). *Proc. Roy. Soc.* B, **127**, 543–76.

van Slogteren, E. (1955). *Ann. appl. Biol.* **42**, 122–128

SEROLOGICAL DIAGNOSIS OF PLANT VIRUS DISEASES

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(With Plate 4)

It is about twenty years ago, that one of my colleagues in Holland said to me: 'Our virus-problems are practically solved now Stanley has found that the virus is a dead protein.' My answer was: 'I do not know how far the problem of the virus may be solved now, but in any case our problems of the virus diseases of our plants are still there.' Although much may be added to our knowledge since then, I believe we still are in about the same position. While preparing this lecture some days ago, studying the programme of this conference and seeing my name between two of your able experts Bawden and Kenneth Smith together with D. Holmes, it seemed to me carrying coal to Newcastle, that I should try to bring a contribution on the virus problems here to-day. Speaking, however, to the Association of Applied Biologists, I shall give a summary of a part of the application of the work done by many scientists from all over the world, for the controlling of the virus diseases in our horticultural and agricultural crops.

I shall not discuss the borders between pure and applied science, because in my career I have not been able to discover them. I only may say that in 1925 Dr Erwin Smith, the doyen of the American plant pathologists, visiting our laboratory and seeing the work we had done, wrote in our visitors' register the words: 'The best is where science can be reduced to practice as you have done it here. With my best wishes for continual success, Sincerely yours, Erwin J. Smith.' This kind remark of Erwin Smith concerned our work on the combating of the bacterial disease of hyacinths.

Now I shall try to give you in a nutshell the reduction of science to practice that we have done for the combating of virus diseases in our stocks, first of flower bulbs and other horticultural crops, and later of different agricultural crops. As probably always is the case we have found again that the pure scientists had left the difficulties at a point where ours begin. There is practically no field of biological sciences where the worker on applied science, in trying to solve his problems, is not himself obliged to build up or strengthen the fundamentals of our knowledge. The field of the worker on plant serology is no exception to this rule and he must have at his disposal all facilities and instruments for fundamental research.

In combating the virus diseases in our stocks of flower bulbs, we had to face the fact that there is practically no cure for a virus-infected plant. The vegetative propagation of the stocks made even a slight infection very dangerous and the only possible way to save a stock was the earliest possible removal of infected or even suspected plants. An early and sure diagnosis was essential for this. The symptoms often are hardly trustworthy for an objective diagnosis. The classical method of infection experiments was not very helpful. Even where we did know the vector or the way of mechanical transmission, the incubation time was about a full year. We practically never got current-season symptoms and we did not know indicator-plants that could help to accelerate the diagnosis. It was therefore sheer necessity that obliged us to look for other possibilities, and so we came to the plant-serological diagnosis of virus diseases of plants.

Good fundamental work in this field was done by Dvorak, and especially by Purdy Beale and Chester, later on by Bawden and Kleczkowski and many others. The value of serological methods for the study and the combating of virus diseases of plants is apparent to all who have used them, although they also realize only too well that it never will be a panacea for the solution of all difficulties. I am sure, however, that the somewhat complicated technique, together with the needed instrumentarium, has been too much of a deterrent for the general use of plant-serological diagnosis. Neither those difficulties, nor the limitations of its applicability however may be reason for the neglect of its possibilities.

Merits

The serological diagnosis is: (1) independent of the symptoms; (2) quick and objective, (3) gives the possibility of identification and classification of many viruses, (4) can help to determine the concentration of a virus in a plant together with its localization and transport in the plant. So it has become an essential and indispensable link in research on viruses and plant-virus diseases, together with the electron microscope, ultracentrifuge, electrophoresis, paper-chromatography, etc. Many of you certainly are aware of this. I want, however, to stress especially the fact that its quickness has made possible its application for freeing potato crops from disease. In our country every year more than a million mother plants for the production of healthy seed potatoes are serologically tested, and one of our sub-stations has attained a capacity of testing 21,000 samples a day. Because of this capacity all the testing can be done in a period of 3 or 4 weeks before lifting. If this testing had to be done along the old way of using test-plant infection or tuber-indexing methods one would be obliged to start early in the spring and the possibility of later infections during the growing season must be accepted. Further, the serological diagnosis can be a great help for: (1) speeding up the breeding of immune varieties; (2) the disentangling of complex virus diseases; (3) above all for the discovery of unknown viruses.

Principles

The principles of the serological method are, as stated by Topley and Wilson and elsewhere by Bawden, very simple.

The blood serum of human beings or animals which have survived an infectious disease contains substances which render them immune to a later infection with the same micro-organism. These substances are called *antibodies*, and the infecting agent that provoked their origin is the *antigen*. The most important fact is that the antibodies react specifically with the antigen that caused their production, and those specific reactions may be observed *in vitro*. So an antiserum containing the antibodies can be used to detect and identify its antigen. We can make this antiserum by injecting an animal using a virus as antigen.

I shall not say more on these principles. I quite agree that they are simple indeed. If I go into details, however, it could be as the story of the clergyman, who said to his congregation: 'Sisters and Brothers, this may seem very simple and clear to you. Wait however till I have preached an hour about this and you will be astonished how difficult and obscure it has become to you.'

However, it is not always sunshine and a bed of roses for the plant serologist, and there are a lot of difficulties and limitations. Many viruses do *not* work as antigens. Sometimes the concentrations of the virus may be too low, or the virus is too unstable to stand handling, or tannins present in the tissues of the infected plant may destroy the virus when we have expressed it in our presses or divided it up in our homogenizers.

Although it may be possible to overcome in the future some of the limitations, we must for the moment be content to apply our method to a limited number of virus diseases. We certainly are fully occupied with the improvement of our technique on this limited field. We have succeeded up to the present in making about twenty-five different antisera (see Table 1).

The methods of the plant serologist are for the most part running parallel with those of the investigator of the virus itself or with those of the biochemist. The crux of the problem is to a great extent the difficulty in extracting the virus antigen from the juice of an infected plant and in purifying and concentrating it without loss. Salting out of the proteins with ammonium sulphate, extracting with chloroform or other chemicals, ultra-centrifugation, freeze-drying and refrigeration have to be tried. It will be evident that, after injecting the crude sap of the diseased plant, the formation of antibodies will be provoked not only by the virus antigens but also by the normal antigens of the healthy plant as well.

The antiserum for this reason will react positively with any healthy or diseased plant that contains the normal antigens. It therefore has to be absorbed with a varying quantity of the juice of a healthy plant before it can be used to test a suspected plant for the presence of the homologous virus antigen. This absorption with healthy plant sap may entail a considerable dilution of the antiserum. So it is advisable to remove as much as possible of the normal proteins before immunizing the rabbits. A lucky circumstance is the fact that in general the virus proteins have a stronger antigenic power than the normal proteins of the healthy plants.

Another obstacle that makes purification necessary may be the toxicity of the plant juice. Again the alkaloids or other poisonous substances have to be removed without the loss of the virus antigen itself. Concentration of the virus antigen is often necessary to get a sufficiently effective antiserum. In some cases these difficulties may be partly overcome by propagating the virus on another host that is not serologically related to the host to be tested, or is less toxic for the rabbits.

TABLE 1. *Antisera prepared in the Laboratory for Flower-bulb Research, Lisse, Holland*

Crop	Virus	Precipit. reaction	Agglutin. reaction
Daffodils	Yellow Stripe	+	–
	Mosaic	+	–
	Chocolate Spotting	+	–
	Silver-leaf	+	–
Hyacinths	Mosaic	+	–
Tulips	Breaking	+	–
	Augustaziek *o*	+	–
Iris	Mosaic *x*	+	–
Lily	Mosaic	+	–
Crocus	Mosaic *x*	+	–
Freesia	Mosaic	+	–
Carnation	Mosaic	+	–
Chrysanthemum	Mosaic	+	–
Sugar beet	Virus-yellow	+	–
Tobacco	Mosaic +	+	+
	Ratel + +	+	–
	Necrosis *o*	+	–
Tomato	Mosaic +	+	+
	Aspermy	+	+
Onion	Mosaic	+	–
Potato	Aucuba	+	+
	X virus	+	+
	Y virus	+	+
	S virus	+	+
	Stengelbont + +	+	–
Dahlia	Mosaic	+	–
Alfalfa	Mosaic	+	–

Selection of a special host that has a higher concentration of virus may improve the titre of the antiserum. We prepare, for instance, our antiserum against the virus of virus-yellows of sugar beets on a hybrid between a sugar beet and a fodder beet (Rijkmaker) that has a considerably higher virus content.

The prepared antisera can be kept in a refrigerator and are at any time of the year available for testing suspected plants. The antigen-antibody reactions can be observed in different ways. The first method of precipitation in small test-tubes we have abandoned because it demands too great a quantity of antiserum. We have replaced it by a micro-precipitation test, described in one of our earlier publications.

A great improvement again has recently been introduced by van Slogteren jun. (1954*b*). He covers the bottoms of a Petri dish with a hydrophobic transparent film of some plastic preparation. The droplets of a mixture of antiserum and antigen are put on this layer and do not spread out. The droplets are covered by gently pouring a layer of paraffin over them from one side of the dish. Between 60 to 100 reactions can be made in one Petri dish, which saves not only a lot of time, but also much space in the incubator.

Another recent improvement introduced in our laboratory by van Slogteren jun. (1954*c*) was the application of the gel-diffusion method for the serological investigations of plant viruses. This was an application of a method used in the medical serological research by Björklund (1952) and Ouchterlony. It is based on the diffusion towards each other of antigens and antibodies in agar or gelatin gels and the formation of precipitation lines. From the work done so far it looks as if this technique is especially suited for the study of small-sized viruses and possibly for the study of normal plant antigens as well. Most of the results of our work and its application to the certification of our potato crops depend on our agglutination test. The virus is adsorbed by the chloroplasts and if these are mixed with a homologous antiserum an agglutination of the chloroplasts can be observed. For this we use small hand presses and mix on a microscope slide five drops of absorbed antiserum with a drop of the juice of the plant to be tested. For serial testing on the assembly line serial presses have been constructed. The high capacity of testing so many samples a day mentioned before is due to this reaction.

It will be evident that for the application of this method on such a large scale in the first place a great quantity of antigen must be available. The antiserum for the virus X of potatoes has been made in horses, and we have been able to make a polyvalent antiserum that can be used to test in one reaction on the viruses X, Y, S and *Aucuba*-mosaic. The great quantity, however, has been used for the testing on X and S virus, and for this purpose we delivered to our research stations about 160 l. of absorbed antiserum last year. Referring to the S virus I must finally ask your attention for one of the merits of the serological method already mentioned before, the possibility of discovering hitherto unknown latent or semi-latent viruses.

Some years ago (de Bruyn Ouboter, 1951), in trying to prepare an antiserum against potato virus A, and using for this the variety Light Industry, a carrier of potato virus A, we got an antiserum that reacted positively with an antigen that could not be virus A. We had to suppose another unknown virus to be present, and later we found in a part of a stock of potato Bintje plants that showed faint virus symptoms, that could not be caused by virus X. These plants reacted positively with the antiserum we had got from the variety Light Industry, and Rozendaal (1952, 1954), after some failures, could prove a virus to be present that could be transmitted by tuber-grafting. Hereafter, we found the virus present in a great number of the stocks grown for the production of seed potatoes. A few of these stocks proved to be 100% infected, but by careful testing and selecting with our antisera we succeeded in freeing the great majority of our stocks from infection. In Table 2 you will find a list of the varieties of potatoes now grown free from X and S virus.

TABLE 2. *Varieties of potatoes grown in Holland and free from X, S, A, and* Aucuba-*Virus.*

Ackersegen
Alpha
Ari
Arran Banner
Barima
Bea
Bevelander
Bintje
Doré
Eigenheimer
Blauwe Eigenheimer
Erdgold
Froma
Frühmölle
Furore
Gineke
Ideaal
Ijsselster
Irene
Konsuragis
Koopman's Blauwe
Koopman's Bonte
Libertas
Majestic
Matador
Meerlander
Noordeling
Noordstar
Orion
Pimpernel
Populair
Primula
Prinslander
Prof. Broekema
Profijt
Prudal
Record
Regina
Rode Star
Saskia
Sientje
Sirtema
Souvenir
Surprise
Thorma
Ulenborgh
Ultimus
Up to Date
Urgenta
Voran
Wilpo
Zeeburger

TABLE 3. *Potatoes: carriers of the virus*

Variety	X	S	A	*Aucuba*	Raised in
Duke of York	+	+	–	–	Scotland
Red Duke of York	+	+	–	–	Mutated in the Netherlands
Industry (dark)	–	+	–	–	Germany
Industry (light)	–	+	+	–	Germany
Kotnov	–	+	–	–	Czecho-Slovakia
Katahdin	–	+	–	–	America
Kenebec	–	+	–	–	America
White Rose	+	?	–	–	America

This virus S, which according to our potato specialists gives a loss of about 15% of profit, proved to be present in a great number of potato stocks all over the continent of Europe. In a publication of the Station of Trevarez (France) Levieil gives a list of 117 varieties of potatoes he considers to be carriers of the S virus. We are not acquainted with all these varieties, but of twelve of them we have stocks free from S virus. An American scientist, specialist on potato viruses, working in our country for some months, brought with him twelve samples of the best available potato stocks. All varieties but one proved to be 100% infected with potato virus S. In Pl. 4 you will see some electron-microscopical photographs of this virus.

Until now it has not been possible to transmit the virus to *Nicotiana tabacum*, or to other easily propagated host plants. The virus probably is mechanically transmitted just as potato virus X is. In any case a sure transmission by an aphid vector has not yet been established. The virus recently described by Kassanis (1954) as latent in carnations may be identical with or related to our virus S. The preparing of the antiserum by immunizing rabbits with it has given considerable difficulties, probably because of the presence of haemolytic or haemo-agglutinating substances in the juice of the potatoes containing the virus. Recently we have succeeded in purifying the virus sufficiently to prevent too great a mortality among the rabbits that are used (1954*a*). Samples of our anti-S virus serum have been sent to many countries. Here the serological diagnosis may possibly give an opportunity to save the stocks that are still partially free, as was the case in our country. In one of our latest publications on the viruses of Freesias we have described the unravelling of virus complexes by means of the serological reactions (v. Koot *et al.* 1954).

I expect that the discovery of the S virus probably may be followed by the finding of other viruses, that till now have escaped our attention.

REFERENCES

BJÖRKLUND, B. (1952). Serological analysis of components in hemopoietic tissue. *Proc. Soc. exp. Biol. a. Med.*, **79**, 319–324.

DE BRUYN OUBOTER, M. P. (1951). A new potato virus. *Proc. of the first conference on Potato virus diseases.* Lisse-Wageningen.

KASSANIS, B. (1954). Some properties of four viruses isolated from carnation plants. *Ann. appl. Biol.* **43**, 103–13.

VAN KOOT, Y., VAN SLOGTEREN, D. H. M., CREMER, M. C. & CAMFFERMAN, J. (1954). Virusverschijnselen in Freesias. *Tijdschr. PlantenZiekten*, **60**, 157–192.

ROZENDAAL, A. (1952). Nieuwe virusproblemen bij de aardappel. *Meded. N.A.K.* **8**, 94–98.

ROZENDAAL, A. (1954). De betekenis van verschillende virusgroepen voor de teelt van pootgoed. *Landbouwvoorlichting* **11**, 299–308.

VAN SLOGTEREN, E. (1952). The serological diagnosis of plant diseases caused by viruses. *Report of the thirteenth International Horticultural Congress.* London.

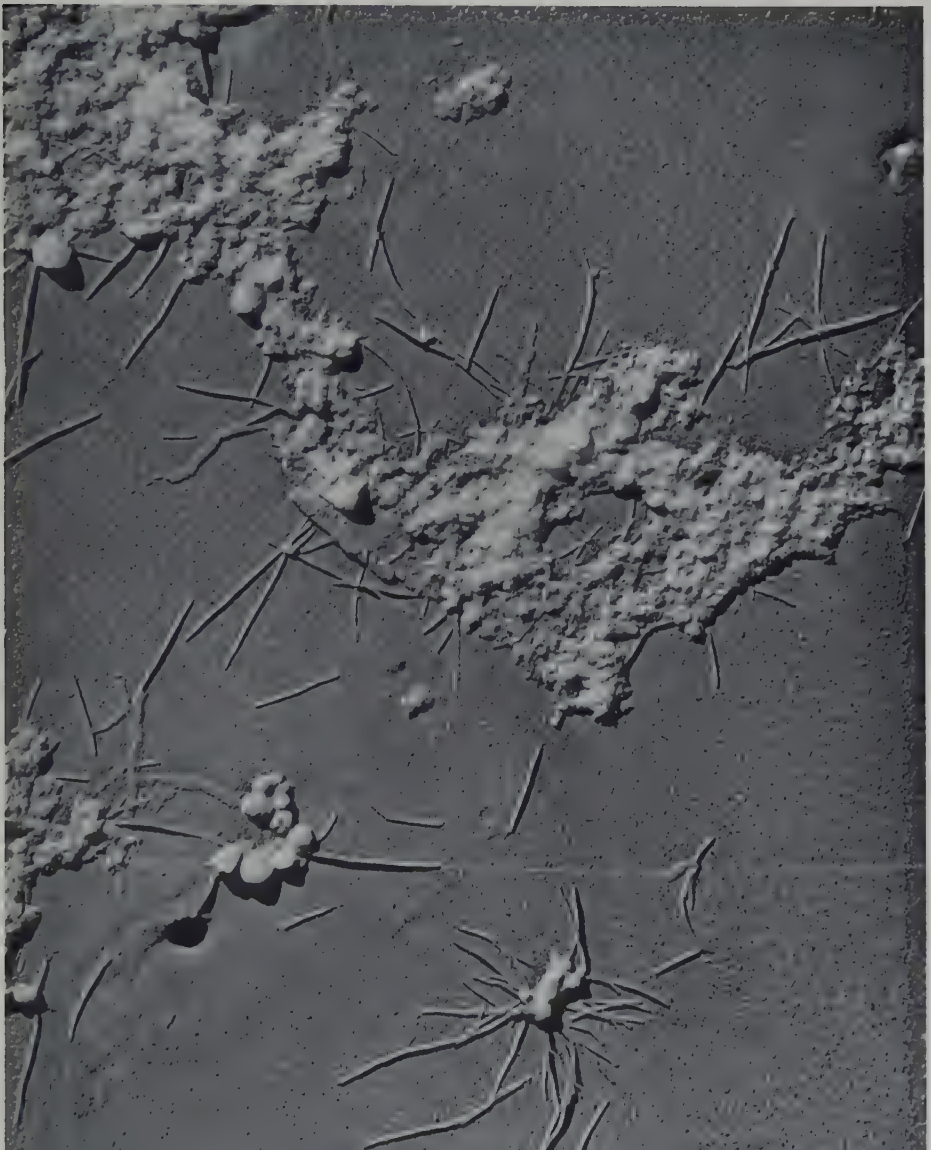
VAN SLOGTEREN, D. H. M. (1954*a*). Preparation of antisera against potato virus S with special reference to the preparation of non-toxic virus suspensions for the immunization of rabbits from extracts of infected potato plants. *Proc. of the second conference on Potato virus diseases.* Lisse-Wageningen.

VAN SLOGTEREN, D. H. M. (1954*b*). Serological micro-reactions with plant viruses under paraffin oil. *Proc. of the second conference on Potato virus diseases.* Lisse-Wageningen.

VAN SLOGTEREN, D. H. M. (1954*c*). Serology of some plant-viruses with the gel diffusion method. *Proc. of the second conference on Potato virus diseases.* Lisse-Wageningen.

EXPLANATION OF PLATE 4

Rod-shaped particles associated with virus-S-infected potatoes in a partially purified preparation (× 20,000).



van Slogteren—*Serological diagnosis of plant virus diseases*

(*Facing p.* 128)

HOLMES, F. O. (1955). *Ann. appl. Biol.* 42, 129–139

ADDITIVE RESISTANCES TO SPECIFIC VIRAL DISEASES IN PLANTS

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Natural selection tends to produce resistant varieties among plants. This occurs when plant species are injured by specific diseases to the extent that they are significantly hindered in their development after infection. Individual plants that differ enough from their parental lines to be somewhat tolerant of each disease can compete to advantage with their more seriously affected neighbours. They become the successful parents of subsequent generations.

This favourable effect of natural selection for resistance in the host is offset, however, by competition and selection for increased virulence among the variants of etiological agents of disease. The counteracting process of selection among pathogens may nullify advantages temporarily gained by host plants. In this dual progression, more resistant plants but also more virulent bacteria, fungi, viruses, and parasites of all kinds are produced. The outcome of the two simultaneous processes of natural selection tends to be a balanced condition of moderate damage to the host and moderate multiplication of the corresponding pathogen. Neither host nor parasite is able to dominate completely or to achieve complete control, but a dynamic balance is reached. This result seems to satisfy the demands of nature. It is not necessarily an adequate solution for the agriculturist concerned with growing a plant crop.

Crowding of plants under cultivation, especially with the use of single varieties or inbred lines rather than mixtures of species for most crops, increases the need for high grades of resistance. Diseases spread from plant to plant so readily in crowded pure stands of crop plants that moderately resistant varieties may be no more capable of combating disease under these circumstances than are more susceptible lines under conditions of scattered and mixed stands in nature. Obviously the farmer needs and wants as many high-grade resistances to disease as possible among his crop plants. Complete immunities would be still better. The problem is how to get high grades of resistance or complete immunities in specific instances.

Complete immunities, though, are far from rarities in nature. We may say as a generalization, in fact, that most diseases are altogether unable to attack most plants. The same kind of generalization applies to diseases of animals, with equal force. The truth of this becomes evident when we consider the number of diseases of very limited host ranges. Many diseases are known as yet in but a single kind of host. Innumerable related species, related genera, and related families may be entirely immune. Many diseases also are known to attack only representatives of single genera or of single families. Some, of course, attack representatives of several or many families. It is the rare exception rather than the rule to find a disease capable of affecting a high percentage of plant species or of animal species that are experimentally or naturally exposed to it.

Notwithstanding the frequency with which complete natural immunity is met in nature, we may well doubt whether it is attained ever through natural selection. A disease may reduce the vigour of its host and the ability of the host to reproduce freely. Thus a bias is established. As has been indicated, any host mutation that is capable of hampering the pathogen may result then in displacement of the original and highly susceptible variety of the host in favour of the new and somewhat more hardy and resistant type. The pressure of natural selection is relieved, however, when a relatively resistant but still somewhat susceptible stock has been developed. Competing species have their own diseases to combat. Moreover, a tendency of the host plant to wander away from its pathogens spatially, at times, probably acts as a safety valve that prevents the establishment of excessive selection pressure.

Not only is it improbable that complete natural immunity is ever an outcome of natural selection, but natural immunities may differ in other ways from the partial resistances that have been established so frequently by plant breeders. What then is the genetic nature of natural immunity? We really do not know.

We know much more about partial resistances. These resistances in many cases have been established in cultivated plants and brought into practical use through genetic studies. A substantial number of these lesser resistances have been concerned with lowered susceptibility to infection, with depression of the rate of reproduction of the pathogen after infection of the host, or with reduction in the ease with which the pathogen can leave the first invaded host to become established in a nearby healthy individual. These interferences with the cycle of disease often have proved dependent on one or a pair of genes or at all events on a small number of genes. Some of the individual genes governing resistance have acted as Mendelian dominants and others have behaved as recessive characters. Occasionally their several effects have proved additive.

It would not be unreasonable to imagine that the many examples of complete immunity to specific diseases in nature may constitute *random assemblages of similar genetic mechanisms in groupings of a higher order*. Let us suppose, for example, that a plant naturally immune to a given disease possesses not one or a few genes that would tend to hamper the causative agent but a great number, such as twenty or forty, of such hindering characteristics. Under these circumstances the pathogen may be entirely unable to make any observable growth even if brought into contact with wounded tissues. We should then have what we would call a natural, or species, immunity. Alternatively, we might reasonably assume that genic differences could in some cases be few, but exceptionally profound. Both explanations may be correct in individual cases but the latter perhaps is not commonly applicable, for single genes have been shown to control numerous partial resistances but very few natural immunities.

An example of one complete immunity that depends on a single dominant gene may be cited, however. Instead of contradicting the hypothesis just offered, it tends to support it.

Wade & Zaumeyer (1940) found that some varieties of the common bean (*Phaseolus vulgaris* L.) are apparently immune to attack by alfalfa-mosaic virus (*Marmor medicaginis* H.). Other varieties are susceptible to infection on experimental inoculation. The experimentally susceptible varieties permit virus to become established and to multiply moderately at the site of inoculation, killing enough cells to produce small necrotic local lesions. The immune varieties possess two independently segregating dominant genes that are lacking in the experimentally susceptible lines. In the progeny of crosses between immune and susceptible parents the presence of either of these dominant genes confers immunity. Perhaps we really are observing here the action of two of a considerable number of genes collectively responsible for the final immunity. The probability that this is true is increased by the observation that even the experimentally susceptible, doubly recessive lines in this investigation proved so resistant in the field that no disease entity could be demonstrated on natural exposure to infection. The exposure in these tests was such as would readily establish alfalfa-mosaic disease in truly field-susceptible species like the garden pepper (*Capsicum frutescens* L.) or Ladino clover (*Trifolium alba* L.). Obviously, in this case at least, no bias in favour of wholly immune individuals would be established under natural exposure because both the immune and the experimentally susceptible biotypes would be, for all practical purposes, equally free from damage by the pathogen. This specific case tends therefore to support, rather than to refute, the idea that complete immunity may be the result of random associations of genes, and that it is not ordinarily established by single, or successive, mutations followed by natural selection.

If these considerations are sound, we may reason from them that intentionally assembling minor resistances to a disease eventually would achieve complete hereditary immunity if carried somewhat beyond the state that would tend to be established by natural selection. This would be of great significance to us at present, for past investigations have exploited many of the effective resistances to disease that depend on single genes or on pairs or small groups of genes. We are faced now with important diseases for which no substantial sources of resistance are known. Can we construct powerful systems, conferring strong resistances or complete immunities to specific diseases, by combining numerous genes of almost negligible individual effectiveness?

To test this possibility we may turn to what is currently becoming known about some of the most readily studied of plant diseases. For maximum progress in development of methods we are forced to choose such examples. Within equal limitations of time and facilities for investigation we would make much less progress in the development of experimental methods by attack on difficultly investigated diseases than by equivalent effort expended on easily studied ones. Thus an attack on the mechanically non-transmissible, tree-affecting peach-yellows disease, however much needed, would not be expected to yield so many useful methods for each man-year of study as the investigation of diseases of short-lived host plants, especially if the causative agents of these were mechanically inoculable, readily extractable, and quantitatively measurable.

ADDITIVE RESISTANCES TO SPOTTED WILT IN TOMATO

Encouragement comes from recent studies of tomato spotted-wilt disease, although the goal of complete immunity has by no means been reached in this instance. Spotted-wilt disease, first described by Samuel, Bald & Pitman (1930) in Australia, originally proved capable of severely damaging all known varieties of the cultivated tomato, *Lycopersicon esculentum* Mill. Later a few varieties were found resistant to the disease in special areas, but these proved susceptible when exposed to viral strains occurring elsewhere. Thus the variety Pearl Harbour was adequately resistant in the Hawaiian Islands (Kikuta, Hendrix & Frazier, 1945) and the varieties Rey de los Tempranos and Manzana proved adequately resistant in New Jersey (Holmes, 1948). All three of these locally resistant lines proved susceptible in parts of Australia. Nevertheless, Finlay (1952), in Western Australia, found that the F_1 hybrid between the Pearl Harbour and Rey de los Tempranos tomatoes produced a useful crop of fruit when both its parents, as well as all other tested F_1 hybrids and their parental varieties, were overcome by disease. Eventually, Finlay (1953) analyzed the resistant hybrid and found evidence for the existence in it of five genes, each effectively controlling a group of viral strains under Australian conditions. Only two of these genes had been recognized previously, one in the Hawaiian Islands and one in New Jersey. These two were ineffective by themselves in Western Australia and might have been discarded there as practically useless had not independently initiated investigations of hybrid vigour called attention to the advantage of their juxtaposition in a hybrid line and to the association of each of them with other genes for resistance, perhaps preserved with them as a result of earlier natural selection in the presence of the disease.

ADDITIVE RESISTANCES TO MOSAIC IN TOBACCO

Tobacco-mosaic disease has been studied continuously by a succession of investigators since the early researches of Mayer (1886) and Iwanowski (1892). A great deal has been learned both about this disease and about its causative agent, tobacco-mosaic virus (*Marmor tabaci* H.). Probably no pathogen is better known morphologically, chemically, physiologically, and genetically than this much studied virus, yet we shall find that we have many more lessons to learn from it. The great amount of study that has been expended on this virus has provided a wealth of useful techniques for further investigation. This makes additional progress much easier than would be the case with a less-studied etiological agent of disease.

Susceptibility of tobacco (*Nicotiana tabacum* L.) as a potential host of tobacco-mosaic virus is not a single attribute. This will become obvious presently from a consideration of the manifold resistances that may be developed through modifications of the susceptible state.

We may define susceptibility as the presence of a series of attributes collectively favouring a disease cycle. A plant disease prospers when entrance of the pathogen into each new host individual is very easy, when multiplication of the pathogen in the host is rapid and prolonged, and when the pathogen is readily freed from the first infected host plant to enter others. A cycle of disease may have other refinements, such as relationships of the etiological agent of disease to arthropod vectors, but these three elements represent the primary portions of the cycle. Establishment of resistance or of immunity generally depends on some change or series of changes that can hamper one or more of these three fundamental processes: of entering a host, multiplying in it, and escaping to infect another individual.

Tobacco may be chosen as a plant almost ideally susceptible to tobacco mosaic. At least, that was true prior to 1933 when the first resistant variety was reported by Nolla & Roque. Before that date, all tested varieties of tobacco displayed what may be called a mottling-type response. This response represents a very high degree of susceptibility. Mottling-type plants become infected with the greatest ease, requiring only light abrasive contacts to wound one or a few cells in the presence of virus from a previously infected plant. Once infected, a mottling-type tobacco plant provides an almost ideal environment for multiplication of the virus, which increases very rapidly and eventually constitutes more than 10% of the dry weight of the infected plant (Bawden & Pirie, 1946). The virus comes to be distributed almost, though not quite, uniformly throughout the plant. It is abundant in leaves, flowers, stems and roots. It is less concentrated in green parts of mottled leaves than in yellowed parts, is less abundant in very young than in mature tissues, and seems absent from the embryos of seeds, but these are not unfavourable factors in its experimental manipulation; in fact, absence of transmission of virus through seeds is favourable to production of healthy seedlings for experimental studies. For transfer of disease from plant to plant, the slightest wounding by abrasive contacts suffices to liberate innumerable viral particles that are ready to enter and multiply in new plants of the susceptible population.

If we indicate by the number 5 a maximum of susceptibility to infection and by the same symbol the most favourable conditions for multiplication and spread of the virus within the plant, as well as the easiest recovery of virus for transmission to a new plant, the almost ideal characteristics of mottling-type tobacco as a potential host of tobacco-mosaic virus may be expressed by the simple formula 5, 5, 5. Lower numbers in the scale may be used in describing resistant varieties, to picture respectively their decreases in susceptibility to infection, to the production of an abundant reservoir of virus in the plant, and to liberation of the virus to infect new plants.

The question whether a plant originally regarded as so ideally susceptible as tobacco once was to tobacco mosaic can be transformed now or in the near future into a naturally immune species is made more significant by the observation that all its tested relatives within the genus *Nicotiana*, and almost all tested species in its family, the Solanaceae, are susceptible to infection to a greater or lesser extent under experimental conditions. Although varieties of tobacco can be grafted on to a great variety of solanaceous plants, they can be hybridized with relatively few. So far as present techniques go, we are limited to hybridizations within the apparently altogether susceptible genus *Nicotiana* and perhaps the neighbouring, and also susceptible, genus *Petunia*. Even the closely allied and susceptible genus *Browallia* now seems too distantly related for successful hybridization with tobaccos. As techniques are improved, this limitation may be modified or removed. For the present it means that immunity, if attained, must transcend any single protective mechanism established through natural selection among the close relatives of tobacco in nature.

Not all *Nicotiana* species have been tested for resistance or grade of susceptibility as yet. If a more nearly immune species exists in nature it probably is growing now in South America, most likely in the region of Peru or Bolivia, where the greatest proportion of partially resistant species are native (Holmes, 1951).

The degree of resistance known among species in the same genus as tobacco may be illustrated briefly as follows:

N. clevelandii	5, 5, 4	*N. raimondii*	5, 3, 3
N. glauca	5, 3, 3	*N. rustica*	5, 2, 2
N. glutinosa	4, 1, 1	*N. sylvestris*	5, 5, 5
N. paniculata	5, 5, 4	*N. tomentosiformis*	5, 5, 4

The last two species in this list are regarded as having descended from the ancestral diploid types that combined their respective sets, each of 12 chromosomes, to form the amphidiploid species *Nicotiana tabacum* ($n=24$). The species *N. tabacum* is not known to-day as a wild species but only as the cultigen tobacco, which is preserved from extinction by man's annual efforts as an agriculturist. The high degree of susceptibility already described as characteristic of tobacco is readily understood by reference to the susceptibilities of these two most closely allied wild species. Moreover, possibilities for its improvement are pictured by the lesser susceptibilities of some of its more distant allies, especially *N. glutinosa*, which possesses the experimental susceptibility 4, 1, 1, but a field-type immunity, 4, 1, 0 as a result of the complete absence of transmission of the virus from plant to plant except by careful grinding and rubbing procedures that are essentially confined to laboratory practice. Despite the fact that the genus *Nicotiana* possesses an array of partial resistances, we have not even a suggestion of a state approaching complete natural immunity, since such field-immune species as *N. glutinosa* are readily infected by virus from other species.

Among flowering plants as a whole, however, and even among the herbaceous dicotyledonous plants that have been most studied, immunities are common. Thus among 310 species of herbaceous dicotyledonous plants tested by Holmes (1946) 111 species showed apparently complete immunity to attack by tobacco-mosaic virus; 100 species, after experimental inoculation, showed local increase of virus without obvious lesions; 15 species showed systemic spread of virus but no obvious lesions; 27 species showed obvious local lesions but no spread of virus; and 57 species showed systemic disease. Thus only 57 of the 310 tested species approached the high degree of susceptibility that is recognized in tobacco. On the other hand, 111 of the same series of 310 species appeared to possess complete natural immunity. The other 142 species possessed various but substantial degrees of resistance, probably adequate in almost all cases for their protection in nature.

The conditions imposed by man in growing tobacco are far from natural. They include crowding of plants, uniformity of spacing between rows and between plants in each row, absence of interplanted unrelated species, maintenance of uniform and relatively high degrees of succulence through controlled fertilization, and persistent abrasive contacts during culture (as in handling and setting seedlings, weeding and cultivating plants, controlling attacks of hornworms, removing flower heads, and in some cases harvesting successively ripening leaves). These conditions encourage the disease. They would set a premium on complete immunity rather than on partial resistance. In immune lines, adaptation of the pathogen would be largely precluded, because the virus would gain no foothold at all nor produce variants within the crop. In plants only partially resistant, the normal type of virus may multiply a little and eventually its variants may be numerous enough to supply at least one capable of prospering in the new environment. Natural increase of this one variant may eventually invalidate any resistance previously achieved. The search for absolute immunity has much to recommend it. Moreover, it implies a high aim from which some deviation can be allowed without complete failure in special instances.

As the years have passed, new discoveries have provided us with independent resistances within the species *N. tabacum*. In some cases the relationship of these resistances to similar resistances occurring among wild species of *Nicotiana* were found to be obscure, but in others they were well established. Eventually so many genic mechanisms were found to influence, in one way or another, the responses of tobacco to infection by various strains of tobacco-mosaic virus that the recombination of these mechanisms seemed to offer hope of completely circumventing the abilities of strains of tobacco-mosaic virus to establish themselves at all in the formerly highly susceptible host plant.

In 1933, as has been mentioned, Nolla & Roque described a variety of tobacco that had been discovered in the vicinity of Mt. Tolima in Colombia, just north of the equator in northern South America. This variety, known as Ambalema tobacco, was so tolerant as to appear almost unharmed by tobacco-mosaic disease. Nevertheless, it was fairly readily infected, even by the typical strain of tobacco-mosaic virus, and it permitted a substantial although somewhat depressed increase of the virus in its tissues. Its ability to delay movement of the virus into young developing leaves probably accounts for the observed tolerance and for a substantially reduced availability of virus for transmission to neighbouring plants. Nolla (1938) showed that the tolerance was dependent on the presence of two pairs of recessive genes, $r_{m1}r_{m1}$ and $r_{m2}r_{m2}$. The susceptibilities of Ambalema tobacco and of similarly tolerant derivatives of this variety, to infection, increase of virus, and viral liberation may be expressed by the notation 4, 3, 3. This notation, as explained before, would imply a slight reduction in ease of infection, somewhat greater reduction in viral increase and in ease of liberation of virus to infect new plants.

Later a second type of resistance to tobacco-mosaic disease was established in tobacco. Holmes (1938) reported that incorporation of a dominant gene *N* from a related wild species, *N. glutinosa* L., transformed mottling-type lines of tobacco into hypersensitive varieties. These were readily infected but permitted so little increase of virus before the death of infected tissues that transfer of the virus from plant to plant became difficult experimentally and practically impossible under natural conditions in the field. The susceptibilities of the *N*-type varieties of tobacco, as now used in some tobacco-growing areas like Kentucky and Virginia, were at first thought to be best represented by the formula 5, 1, 1 for experimental procedures and 5, 1, 0 for field use. Subsequent studies (Holmes, 1953) have suggested that a better representation would be 4, 1, 1 and 4, 1, 0 for experimental and field conditions, respectively. The appearance of a 0 in these notations gives the first hint that a complete immunity to this and other strains of tobacco-mosaic virus eventually may be achieved in tobacco. Nevertheless, a complete immunity will require corresponding changes in additional susceptibilities because hypersensitive plants, although nearly immune to infection from each other, are still highly susceptible to infection from reservoirs of virus outside the crop and may be seriously damaged by such infection unless appropriate measures are taken to alleviate the harm.

Another type of resistance was reported by Schwartz & Cuzin in 1951. These investigators, working in France, noted that a line of tobacco called Java Isère × Cabot was less easily infected than an ordinary mottling-type variety. Once infected, however, it became chlorotically mottled and a substantial source of virus for infection of other susceptible plants. The slight tendency to escape infection was confirmed by Holmes (1953). The characteristics of this line of tobacco may be summarized by the formula 4, 5, 5.

EFFECTS OF OTHER GENES

Experiments were designed to determine whether the tendency of Java Isère × Cabot tobacco to remain healthy after light exposures to disease had any dependence on genes producing tolerance in Ambalema-type varieties, as would be the case if $r_{m1}r_{m1}$ or $r_{m2}r_{m2}$ should produce a slight resistance to infection when alone as well as a tolerance to the presence of virus in infected foliage when associated as a pair of independently segregating recessive genes. In the course of these experiments the genic control of the tendency to escape infection has not yet been fully disclosed, but several new types of response to infection by various strains of tobacco-mosaic virus were discovered, as well as several hitherto unrecognized effects of previously known genes.

In testing for resistance to infection, a strain of tobacco-mosaic virus known as 1952D was used. This strain of the virus is incapable of maintaining itself autonomously in nature but under conditions of experimental transfer it is capable of producing necrotic primary lesions in any variety of tomato or tobacco that it can infect. Ambalema-type tobacco possesses what seems to be complete or nearly complete immunity to strain 1952D. Here again is a suggestion that immunity to all strains may be achieved eventually. The immunity to strain 1952D was found to follow the segregation of genes $r_{m1}r_{m1}$ and $r_{m2}r_{m2}$, as tolerance to the typical strain does in $r_{m1}r_{m1}r_{m2}r_{m2}nn$-type plants, and to occur also in $NNr_{m1}r_{m1}r_{m2}r_{m2}$ plants. This immunity seemed at first to heighten the probability that reduction in susceptibility as measured in Java Isère × Cabot tobacco might depend on one of the Ambalema genes. If one of the gene pairs were present in Java Isère × Cabot tobacco, the partial escape of infection, but not tolerance, would perhaps be expected. In this case however, a cross between Connecticut Broadleaf Ambalema and Java Isère × Cabot would be expected to yield a 3:1 ratio of mottling-type to tolerant plants in the second generation rather than the 15:1 ratio indicative of a two-gene difference. In 269 plants of such a second-generation hybrid a ratio of 14·8:1 was found, clearly an indication that Java Isère × Cabot tobacco lacks both of the genes co-operatively determining tolerance in the variety Ambalema.

During the study of the tendency to escape infection in Java Isère × Cabot tobacco, it became evident that moderate differences in susceptibility to infection characterized some of the partial resistances previously known but prized in the past only for other attributes. The gene recognized earlier as producing hypersensitivity, with its associated reduction of the effective reservoir of virus nearly to the vanishing point, and one of the two genes controlling tolerance after infection in Ambalema-type tobacco were both separately able to induce tendencies to escape infection and these independent tendencies to escape infection proved additive (Holmes, 1953).

Recent research has disclosed that other genes play a part in determining the exact type of response of hypersensitive tobacco plants to infection by strains of tobacco-mosaic virus. The two recessive genes that determine self-blanching of older stems and lower leaves (g_1 and g_2 of Henika, 1932) disclose their presence also by forming chlorotic haloes around necrotic local lesions. A gene presumed to be the partly recessive n^s of Weber (1951) tends to localize the ribgrass of tobacco-mosaic virus, without perceptibly reducing the number of local lesions established as a result of inoculation.

It has been demonstrated also that thiouracil treatments, such as temporarily reduce the titre of tobacco-mosaic virus in tissues of mottling-type tobacco but are unable to prevent the subsequent development of chlorotic mottling, can co-operate with the hypersensitivity of NN and $NNr_{m1}r_{m1}r_{m2}r_{m2}$ tobacco in such a way as to cure the induced disease if treatments are initiated soon after the development of necrotic local lesions (Holmes, 1954). Untreated plants generally die or are severely stunted as a result of systemic infection, but treated plants soon recover from the blanching effects of daily applications of 5 mg. of thiouracil in 50 c.c. of aqueous solution and grow to maturity, blossoming and setting seed, essentially like uninoculated specimens. Curiously enough, rather short (3- or 4-day) treatments or rather long (10-day) treatments seem more effective than series of applications of intermediate (7- or 8-day) lengths. This observation calls for further investigations to substantiate or refute it.

We still do not know the nature of the genetic control of the tendency to escape infection in the tobacco variety Java Isère × Cabot. In attempting to learn what this may be, we are likely to disclose still more genes that influence the level of resistance and that can be used in concert to provide a heightened resistance or an approach to actual immunity in this once highly susceptible plant.

The next few years of continued study of this and other diseases may be expected to show whether we shall be able to control any, or many, diseases by collecting minor resistances and combining these in such a way as to provide effective protection for plant species that are now regarded as completely susceptible to specific diseases.

REFERENCES

BAWDEN, F. C. & PIRIE, N. W. (1946). The virus content of plants suffering from tobacco mosaic. *Brit. J. exp. Path.* **27**, 81.

FINLAY, K. W. (1952). Inheritance of spotted wilt resistance in the tomato. I. Identification of strains of the virus by the resistance or susceptibility of tomato species. *Aust. J. sci. Res. S.* B, **5**, 303.

FINLAY, K. W. (1953). Inheritance of spotted wilt resistance in the tomato. II. Five genes controlling spotted wilt resistance in four tomato types. *Aust. J. biol. Sci.* **6**, 153.

HENIKA, F. S. (1932). The inheritance of the White Burley character in tobacco. *J. agric. Res.* **44**, 477.

HOLMES, F. O. (1938). Inheritance of resistance to tobacco-mosaic disease in tobacco. *Phytopathology*, **28**, 553.

HOLMES, F. O. (1946). A comparison of the experimental host ranges of tobacco-etch and tobacco-mosaic viruses. *Phytopathology*, **36**, 643.

HOLMES, F. O. (1948). Resistance to spotted wilt in tomato. *Phytopathology*, **38**, 467.

Holmes, F. O. (1951). Indications of a New-World origin of tobacco-mosaic virus. *Phytopathology*, **41**, 341.

Holmes, F. O. (1953). The tendency of some types of tobacco to escape infection by tobacco-mosaic virus. *Phytopathology*, **43**, 475. (Abstract.)

Holmes, F. O. (1954). Preventive and curative effects of thiouracil treatments in mosaic-hypersensitive tobacco. *Phytopathology*, **44**, 492. (Abstract.)

Iwanowski, D. (1892). Ueber die Mosaikkrankheit der Tabakspflanze. *Bull. Acad. Imp. Sci. St Petersburg*, Ser. 4, **3**, 67.

Kikuta, K., Hendrix, J. W. & Frazier, W. A. (1945). Pearl Harbor, a tomato variety resistant to spotted wilt in Hawaii. *Circ. Univ. Hawaii Agric. Exp. Sta.* no. 24.

Mayer, A. (1886). Über die Mosaikkrankheit des Tabaks. *Die Landwirthschaftlichen Versuchs-Stationen*, **32**, 451.

Nolla, J. A. B. (1938). Inheritance in *Nicotiana*. III. A study of the character for mosaic resistance in *Nicotiana tabacum* L. *J. Hered.* **29**, 42.

Nolla, J. A. B. & Roque, A. (1933). A variety of tobacco resistant to ordinary tobacco mosaic. *J. Dep. Agric. P.R.*, **17**, 301.

Samuel, G., Bald, J. G. & Pitman, H. A. (1930). Investigations on 'spotted wilt' of tomatoes. *Bull. Counc. sci. industr. Res. Aust.* no. 44.

Schwartz, D. & Cuzin, J. (1951). Faible susceptibilité d'une variété de *Nicotiana tabacum* vis-à-vis de la mosaique du tabac. *Annales de l'Institut Expérimental du Tabac de Bergerac*, **1**, 167.

Wade, B. L. & Zaumeyer, W. J. (1940). Genetic studies of resistance to alfalfa mosaic virus and of stringiness in *Phaseolus vulgaris*. *J. Amer. Soc. Agron.* **32**, 127.

Weber, P. V. V. (1951). Inheritance of a necrotic-lesion reaction to a mild strain of tobacco mosaic virus. *Phytopathology*, **41**, 593.

Bawden F. C. (1955). *Ann. appl. Biol.* **42**, 140–147

THE SPREAD AND CONTROL OF PLANT VIRUS DISEASES

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Although I have been working with plant viruses for almost exactly half the lifetime of the Association of Applied Biologists, I cannot claim to have contributed much to the subject on which I have been honoured with an invitation to speak at this Jubilee meeting. I take the invitation, therefore, primarily as a tribute to the work of my colleagues, particularly Mrs M. A. Watson, Drs L. Broadbent, P. H. Gregory, R. Hull, B. Kassanis, and Mr J. P. Doncaster.

Dr Kenneth Smith has already outlined the considerable progress that has been made in knowledge about viruses, and my first task is perhaps to stress the fact that there is still very much of which we are woefully ignorant. The relative position of the study of viruses and, say, mycology, is perhaps most vividly illustrated by Dr Smith's statement that only during the last 10 years have we begun to know what any of the viruses look like. Of most, nothing is known about either their sizes and shapes or their constitutions. Contrast this with the fungi; these had not only been seen but the life histories of many had been elucidated, and measures for controlling some pathogenic ones had been established, before the Association of Applied Biologists came into being. Primitive though our subject is, enough is known about the behaviour of viruses to appreciate that modern conditions of agriculture and life tend to favour their spread, and that, unless we learn much more and then apply our knowledge to combat them, virus diseases are likely to become even more important in the future than they have been in the past.

Some of the conditions that favour virus diseases also favour the spread of other kinds of parasite; for example, the cultivation of large areas of a uniformly susceptible crop, the transport of all kinds of plants around the world, and the general increase in the speed and quantity of travel. Even some of these are perhaps more dangerous with viruses than with other pathogens. Whether plants are contaminated with fungi, bacteria, insects or other organisms, can be determined visually, but healthy looking plants only too often harbour viruses that can cause serious diseases in some other variety or species. Methods of inspecting plants can, of course, be extended to cover tests for viruses of whose existence we know, but we must expect that there are far more than these still awaiting discovery.

Two other features of modern horticulture and agriculture, (1) the increasing use of clonal varieties, and (2) the improving standards of manuring and cultivation, seem particularly likely to encourage the spread of viruses. This can be expected from the fact that viruses normally cause systemic infections in the plants they damage and survive in vegetative tissues for as long as these remain alive. The use of clonal varieties entails propagating vegetatively, either by 'natural' reproductive organs like bulbs and tubers, or by pieces of tissue used as scions and cuttings. The uniformity of a high-quality crop that results from vegetative propagation is something that growers cannot afford to forgo, but they should constantly remember that, had methods been expressly designed to perpetuate viruses, the methods would be exactly those used to propagate clonal varieties. To use these varieties safely means that increasing attention must be paid to the health of nursery stocks, for the buyer of new planting material has a right to know that he is at least starting with vigorous and not infected stocks. Recent work with fruit trees suggests that the nurseryman will also benefit from a rigorous clean up of his propagating material, for the slow growth of newly grafted trees, and failures of scions ('incompatibility'), are often sequels to either scions or stocks containing a virus. The field certification schemes now applied in many countries to an increasing number of vegetatively propagated plants are wholly admirable and have done much good, but they need extending to still more crops, and visual inspection may need to be supplemented by other tests. I need not stress the value of serology as a cheap and rapid method of testing for many viruses, because Dr E. van Slogteren has already shown how this is now being used extensively in the Netherlands. The prospects of providing virus-free clones, even of those that are now universally infected, look much better than a little while ago, for it now seems that, by such treatments as growing infected plants for some time at temperatures around 37° C. or by culturing the apical meristems of stems, plants can be freed from many viruses, including some that are stable and have high thermal inactivation points *in vitro*.

Most viruses that invade the whole vegetative parts of plants fail to enter the pollen or the egg cell, and the sowing of true seed can usually be relied upon to give virus-free seedlings. The mechanisms whereby viruses are normally excluded from passing into seed is unknown, but when we see how rapidly clones lose their vigour because they accumulate viruses, the evolutionary necessity for such a mechanism is obvious. A virus that regularly passed through the seed of a wild plant in which it causes a serious disease would soon be eliminated, for the infected seedlings could not survive in competition with their more vigorous neighbours. This argument does not hold for viruses in hosts they fail to damage, and it may be that seed transmission is more common with these, though the point has yet to be studied. Also, crop plants are spared much of the intense competition experienced by wild plants and in these coddled plants there is also the possibility of seed-transmitted viruses surviving, even though they damage their host plants. Indeed, some such are already known, and the number is growing, so that in the future it may become necessary to take precautions to ensure healthy parents for crops raised from true seeds, comparable to those now needed for clonal varieties.

Improving standards of manuring and cultivation can be expected to increase the spread of viruses, unless measures are taken to stop it, simply because they will produce bigger and more actively growing plants. The little that has yet been done on factors affecting the suceptibility of plants to infection by viruses suggests that, the better the plants are doing, the more likely they are to become infected. Certain it is that, once infected, a large and well-fed plant maintains a much higher virus population than does a small starved one, and so provides a larger source of infection for other plants. The control of weeds could also increase virus spread, both by leading to bigger crop plants and by making the crop the only host for incoming vectors of viruses. Further, we must remember that the control of some of the other kinds of pests and diseases that used to cripple our crops is making things easier for the viruses. None of these things is, of course, any reason for not growing weed-free, well-fed crops; they all mean simply that, if we are to reap the full rewards of high farming, we must also learn to control virus diseases.

Virus diseases spread in a crop in two ways: (1) by virus that is brought into a crop from outside; and (2) by spread from infected to healthy plants in the same crop. What can be done to control virus diseases that mainly spread from plant to plant within a crop is strikingly illustrated with potatoes. Twenty or so years ago, the aphid-transmitted viruses that cause potato leaf roll and severe mosaic were prevalent, even in the crops of the best potato growers in East Anglia. Now, as a result of the increasingly stringent requirements of seed-certification schemes operated in districts where these viruses spread slowly, coupled with the farmer's practice of regularly getting new stocks of certified 'seed', these diseases are almost rarities, found frequently only in gardens and allotments where the grower keeps his own 'seed'. For a time the certification schemes paid little attention to a less virulent virus, potato 'X', the usual cause of mild mosaic, which was universal in stocks of many varieties and, because of its prevalence, became the most important virus causing loss of yield, for loss is the product of prevalence times virulence and is not to be measured solely by effects on single plants. Now that virus 'X' is also considered in the certification schemes and stocks free from it are supplied, the potential cropping power of potatoes is probably higher than ever before. Virus diseases still cost the English potato grower a lot of money, but the cost is now to be measured in the price of new 'seed' and not in tons of tubers.

It would be rash to think that our troubles with virus diseases of potatoes are over, or that viruses of all other vegetatively propagated crops can also be combated by raising stocks in the districts which produce good 'seed' potatoes. With some it will no doubt succeed. It has so far with stecklings for the sugar-beet seed crop. Since these have been raised in areas remote from other beet, or in some other conditions that prevent them from getting yellows, the average yield of seed per acre has risen from about 10 cwt. to 1 ton. But isolation from viruses is not necessarily the same thing as isolation from diseased crops of the same species. Some viruses have wide host ranges and can make the most disconcerting jumps to hosts in different families or orders. Success with potatoes and sugar-beet stecklings in the north and west of Britain has been achieved because the current virus diseases of these plants are transmitted mainly by one species of aphid and because these districts were fortunately free from other viruses that could move into these two crops. The same conditions cannot be expected to hold generally, and although stocks of other crops raised in these districts will probably escape viruses transmitted by *Myzus persicae*, they may well run into some new ones transmitted by other vectors. Not all new virus diseases need come into a crop from some other species. We know that all plants of the potato variety King Edward, which accounts for more than a quarter of the potato acreage of Britain, contain a virus that cripples many other varieties. At present this virus is an academic novelty, providing harmless fun for those who like to speculate on the origin of viruses, but it is so only because it has no vector. Should some insect that could transmit this virus take it into its head to feed on potatoes, then we should have a new trouble, which might well make our present ones with leaf roll and severe mosaic look trivial. The paracrinkle virus in King Edward potatoes is certainly not the only potential virus that lurks unnoticed, and many of the virus diseases now being newly recorded are probably consequences of some insect enlarging its host range and becoming a vector of something that was previously harmless.

As most of the viruses that commonly affect field crops are transmitted by insects, and there are now effective sprays to control most insect pests, it is reasonable to ask why virus diseases still cause losses and why they are not controlled by insecticides. There is no simple or certain answer; indeed, there is little doubt that some modern insecticides properly applied do decrease the rate at which some viruses spread, but the control of an insect as a vector is essentially a different problem from its control as a pest. To control aphids as pests, for example, it is necessary only to keep an infestation below the numbers at which damage is done, and this means mainly preventing wingless forms from multiplying excessively in a crop. But these are not the main vectors of viruses, for most probably spend their whole life on the same plant, and an insect must move if it is to transmit a virus. Insecticides wrongly applied may actually increase the spread of viruses, for if they do not kill all the insects quickly, they may stimulate wingless ones to move, which can turn them from potential into active vectors. Also, by prolonging the life of potato crops, insecticides have sometimes led to increased incidence of leaf roll, for the sprayed crops have become infested by winged aphids leaving moribund, unsprayed crops.

In Britain viruses of potato, sugar beet, lettuce and cruciferous crops, seem to be spread mostly by the relatively few winged aphids, and these are solely responsible for introducing the prevalent viruses into a previously healthy crop. An insecticide that prevents aphids from multiplying on a crop will obviously prevent any spread of viruses that would have occurred by such insects, but as yet no insecticide is known that will prevent any infective aphids that come into a crop from infecting the plants on which they first feed. Some of the new persistent insecticides also prevent winged aphids from spreading viruses from infected to healthy plants in the same crop, but their ability to do this depends greatly on the manner in which the virus is transmitted by the aphid. Some viruses can be acquired by insects that feed for only a minute or so on an infected plant, and the insect can then immediately infect another plant. At the other extreme, but there are all intermediate grades, are viruses whose vectors need to feed on infected plants for an hour or more before they acquire virus, and the vectors then may not be able to infect a healthy plant for several hours or even days. The spread of this second type of virus within a crop can be largely prevented by spraying with suitable persistent insecticides, but these act too slowly to prevent the spread of the first type by winged aphids or to prevent insects that arrive in the crop already infective with the second type from infecting the first plants on which they feed. It is easy to prescribe what is needed to prevent the introduction or spread of the various kinds of insect-transmitted viruses; there are two choices, either a persistent insecticide that kills vectors immediately they alight, or a persistent insect repellant that will prevent them from alighting. Whether the chemists will find it so easy to supply such substances, however, is another matter.

So far tests with insecticides have been made mainly against aphid-transmitted viruses. This is rather odd, for the leafhopper- and thrips-transmitted viruses are all those whose vectors do not become infective immediately they feed on an infected plant, and *a priori* might be expected to be more amenable to control by insecticides. However, until more is known about the origins of the serious outbreaks of disease these viruses cause, particularly whether they derive mainly from already infective insects entering crops or from spread within the crop after a few plants have become infected in this manner, no confident guess can be made about the value of current insecticides.

Indeed, before we can assess the possibilities of controlling virus diseases by any methods, whether by spraying or such things as varying the sowing date and surrounding with barriers, much more information is needed about the 'ecology' of the viruses. We need to know where they are coming from, what is bringing them, and more about the behaviour of the vectors. It is obvious, too, that insects with sucking mouthparts, which in the past have been regarded as a prime choice in seeking vectors, are not unique in being able to transmit viruses, and a determined search among those insects that bite leaves, or even among animals of quite different orders, will no doubt provide vectors for many viruses whose method of spread now remains unknown.

There are some viruses, which though they may occasionally be spread by some insect, seem primarily to spread either by contact between infected and healthy plants or by cultivators as they work with the crop. First among these is tobacco-mosaic virus, which in Britain causes much loss every year by infecting almost the whole of the tomato crop. It seems to me that virus workers have been rather lax in not testing the effects of sprays on the spread of this virus. Substances have long been known that inhibit infection by this virus, and they obviously warrant testing; if inhibitors were regularly applied from before transplanting to, say, the fourth truss, they might prove valuable prophylactics. Indeed, this year considerable publicity has been given to benefits thought to have derived from spraying with skimmed milk, a readily obtainable substance that is a reasonably good inhibitor of infection in some plants. Unfortunately the publicity may be premature, for the assumed benefits are deduced from experience rather than experiment; the sprayed plants were not compared with unsprayed ones, so that the benefits attributed to spraying could have other explanations. However, the publicity may have the useful effect of ensuring that experiments will be made at last to see whether the obvious potential value of inhibitors can be realized in practice. Certainly the loss now caused by mosaic in tomato and tobacco crops is ample to justify extensive trials to see whether it can be mitigated by spraying with such unusual materials, all innocuous to mammals and some with a certain charm, as milk, sap from such varied plants as carnation, sweet-william, sugar beet, spinach or mushrooms, and extracts of pancreas.

The best method of controlling virus diseases, as of other kinds of diseases, is, of course, to produce immune or resistant varieties. Considerable success has already been achieved with some crops, and we can expect more in the future. When the ideal of immunity cannot be achieved, there are still many different properties that can be bred for; resistance to infection, ability to localize infection or otherwise restrict virus multiplication, ability to tolerate systemic infection, or resistance to a specific vector. How various small factors can sometimes be added together to give a result of practical value has been described by Dr F. O. Holmes, and I need add nothing to his account, except to stress the fact that we must not expect permanent results. Viruses can reach immense populations in systemically infected plants and variants with new pathogenic properties can be expected with even greater frequency than with larger pathogens. However, the continued freedom of such old potato varieties as King Edward and Epicure from virus 'X', which is widespread in varieties that are not hypersensitive, promises well, for it shows that the ability to localize infection can last, at least with viruses that are not readily transmitted by insects.

Virus diseases are individual things and it is little use hoping for a universal panacea. Each will need individual study, and measures that are found successful against one in one crop, or in one locality, will not necessarily succeed in another. There are, however, so many possible lines of attack that, if the diseases are studied enough, there is every reason to think that adequate measures will be found to control virus diseases of annual crops or crops that are meant to stand for only a few years. The outlook is less promising for trees and other perennial crops, of which, unfortunately, more and more serious virus diseases are now being recorded. Peach yellows, sandal spike and Pierce's disease of the grape-vine were about the only virus diseases of such plants that used to cause concern, but now there are swollen shoot of cacao, decline of citrus, phloem necrosis of elm, *court noué* of the vine, and innumerable diseases of apple, apricot, cherry, pear, plum and peach. And there is pathetically little that can confidently be recommended as a control measure, except the classical advice of the plant pathologist, 'dig it up (or cut it down) and burn it'. No doubt this is excellent advice, and if all infected plants could be identified and destroyed it would be effective. Eradication of a pathogen, however, is rarely possible, and a disease will be controlled by felling infected trees in a crop only if the slaughter policy is started early and spread is mainly from tree to tree within the crop rather than into the crop from outside sources.

Virus diseases of perennial crops certainly demand more attention than they have so far received, for their control is going to raise different kinds of problems. Until very much more is known about their rate of spread, how they spread, and where the viruses come from, possibilities are difficult to assess. To produce resistant varieties will take a very long time, and, although insecticides may be useful with crops that are already sprayed regularly or are valuable enough to repay the cost of repeated sprayings, they cannot be expected to keep trees virus-free indefinitely. The difference between spraying against, say, apple scab and a virus disease of apples, is that it does not matter if a tree has one scab lesion, but one site of infection with a virus means that the whole tree will become permanently infected. The treatment of these diseases demands a new approach, and they make the search for chemotherapeutic or prophylactic substances economically worth while, even though the chance of finding them seems faint. And, it must be confessed, the chances are not good. A lucky piece of empiricism, of course, may produce something, but it is better not to rely on this and to work also on the mechanism of virus multiplication so that some rational approach to the problem may become possible. Already, following the knowledge that tobacco-mosaic virus is a nucleoprotein, sulphur-containing analogues of purines and pyrimidines have been found to decrease the rate at which it multiplies in infected plants. This is still very far from successful chemotherapy, and the substances also disturb the metabolism of the host plant, but it is a pointer to future possibilities. To cure a tree will be worth giving it a bad time temporarily. That the physiology of a plant can be so altered that it will no longer support the multiplication of a virus to which it is normally susceptible, and the plant still survive, is shown by the success of heat therapy. Chemotherapy may be equally possible, but it is going to ask a lot of a substance that it should specifically prevent virus multiplication and leave the host unaffected. The few viruses whose chemical constitution is yet known all seem to be nucleoproteins, with their nearest relatives possibly the 'normal' nucleoproteins. They seem to depend on the host plants, not only for their substance, but also for the mechanisms whereby they are synthesized. Other viruses, however, may be chemically more complex, have specific activities of their own, and take a more active part in their own synthesis. If so, they are more likely to prove susceptible to attack by chemicals that do not injure the host. Such speculation, however, is idle in our present stage of ignorance, and I end, as I began, with a plea for more work on viruses, which now provide one of the most fascinating subjects for botanical research. So far in Britain their study has been almost the exclusive prerogative of applied biologists in research stations and research institutes. There is much to be done that would be appropriate to university botanical departments, and it is to be hoped they will join in. When we consider how much they have contributed to our knowledge of fungi and bacteria, we can be sure that, if they will now begin to take an active interest in viruses, whoever talks on the control of virus diseases at the Centenary Meeting of the Association of Applied Biologists will be able to talk more confidently and paint a rosier picture than I can to-day.

Plant growth-regulating substances

Wain, R. L. (1955). *Ann. appl. Biol.* 42, 151–157

A NEW APPROACH TO SELECTIVE WEED CONTROL

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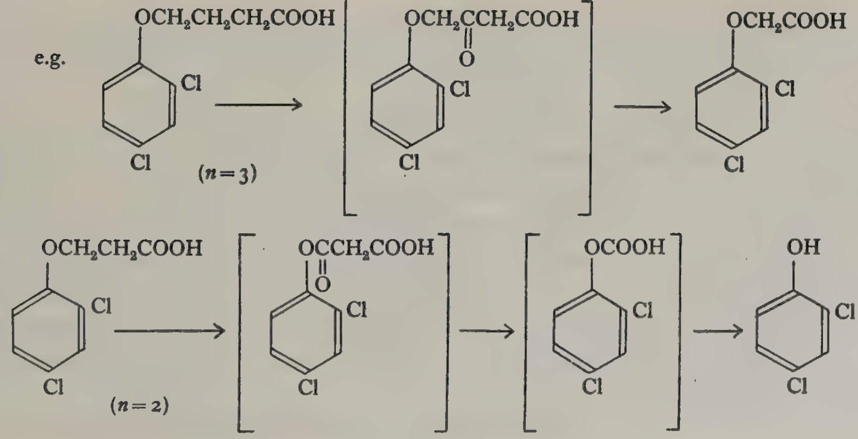
(With Plates 5 and 6)

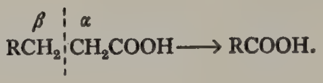
Although plant growth-regulating substances have been studied from various aspects at Wye during the past seven years, our main investigations have been concerned with chemical structure in relation to growth-regulating activity. From this work, which has involved the synthesis and examination of many hundreds of compounds, mainly aryloxyalkylcarboxylic acids, has developed studies on mode of action and competitive antagonism and on the breakdown of certain of these acids within living plant tissues. Much of this work has already been reviewed (Wain, 1953), and it is my purpose to-day to deal only with some of our more recent findings, indicating how these investigations, carried out primarily as an academic study, have led to developments which may prove to be of considerable agricultural importance.

Several workers have demonstrated that the growth-promoting activity of ω-substituted aryl- or aryloxyalkylcarboxylic acids is related to side-chain length and that an alternation in activity may operate as the series is ascended. Thus, Grace (1939) examined the first five members of the ω-(l-naphthyl)alkylcarboxylic acid series for their capacity to promote rooting of cuttings and showed that those compounds with an odd number of methylene groups in the side chain possessed an activity similar to that of l-naphthylacetic acid, whereas the compounds with



an even number of methylene groups had negligible activity. Synerholm & Zimmerman (1947), using the tomato leaf epinasty test, found a similar alternation to occur with increasing length of side chain in a series of seven ω-(2:4-dichlorophenoxy)alkylcarboxylic acids. These workers suggested that degradation of the acids by a β-oxidation mechanism could explain their results. By such means, acids with an odd number of side-chain methylene groups might become converted to the active acetic homologue, whereas acids containing an even number might yield the parent phenol with no growth-regulating activity (see diagram on p. 151). Such an explanation is fully consistent with the alternation in activity which we found to operate in the Went pea test for a series of ω-(4-chlorophenoxy)alkylcarboxylic acids (Fawcett, Ingram & Wain, 1954).

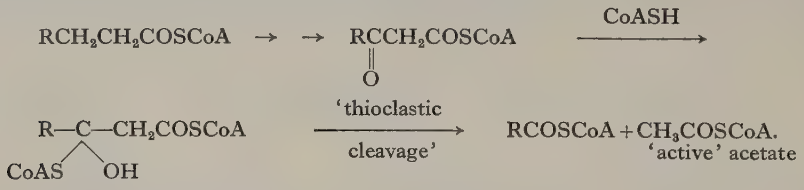
As early as 1904, Knoop had suggested that fatty acids were degraded in the animal body by a process involving oxidation at the carbon atom in the β-position to the carboxyl group.



$$\overset{\beta}{RCH_2}\,\vdots\,\overset{\alpha}{CH_2}COOH \longrightarrow RCOOH.$$

There is now overwhelming evidence that such β-oxidation does occur in the animal body (e.g. see Breusch, 1948; Fawcett *et al.* 1954). More recent studies (e.g. Lehninger, 1952; Lehninger & Greville, 1953; Beinert, 1953) have indicated that the β-oxidation process involves a number of enzymes which can only act on coenzyme A derivatives of these acids. The fatty acid is thereby degraded into 2-carbon units of 'active' acetate, i.e. acetyl coenzyme A, which can then be oxidized either via the tricarboxylic acid cycle or enter into reactions involving biological acetylation. Alternatively, it may undergo self condensation to form acetoacetic acid.

The fatty acid degradation may be represented thus:



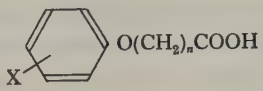
$$RCH_2CH_2COSCoA \rightarrow \rightarrow R\underset{\underset{\displaystyle O}{\|}}{C}CH_2COSCoA \xrightarrow{\text{CoASH}}$$

$$R-\underset{CoAS\quad OH}{C}-CH_2COSCoA \xrightarrow[\text{cleavage'}]{\text{`thioclastic}} RCOSCoA + \underset{\text{`active' acetate}}{CH_3COSCoA.}$$

Although there is now abundant evidence to substantiate the concept of β-oxidation of fatty acids within animal tissues, there has, until recently, been little evidence that this type of oxidative breakdown operates in plant biochemistry. As already indicated, the alternation in growth-regulating activity shown in homologous series of aryl- and aryloxy-acids is explicable on the β-oxidation hypothesis though even here, inconsistencies have been found; for example, Synerholm & Zimmerman (1947) reported that γ-(2:4:5-trichlorophenoxy)butyric acid is inactive, whereas the acetic homologue is highly active in the single test they employed, namely, the tomato leaf epinasty test.

Chemical evidence that β-oxidation may operate within flax seedlings has been obtained in our investigations with members of the homologous series of ω-phenoxy acids $C_6H_5O(CH_2)_nCOOH$, with $n-1$ to 10 (Fawcett *et al.* 1954). These acids were supplied to the seedlings through their roots. After a suitable interval to allow breakdown of the acids to occur, the plants were macerated, steam-distilled and phenol in the steam distillate estimated colorimetrically. It was found that those acids with an even number of side-chain methylene groups ($n=2$, 4, 6, 8 and 10) gave rise to appreciable quantities of phenol, whereas the acids with $n=1$, 3, 5 and 7 yielded only traces of phenol (Fawcett *et al.* 1954). The results are fully consistent with the idea that the side chain of these acids is degraded within the flax plant by β-oxidation. It is of interest that 9-phenoxynonane-l-carboxylic acid ($n=9$) showed exceptional behaviour in yielding phenol, a result which can be explained by side-chain degradation involving ω-oxidation and one which correlates in a striking manner with the results of animal metabolism studies (Fawcett *et al.* 1954).

With this chemical evidence that β-oxidation can occur within plant tissues, our investigations in this field were extended in several directions. First, a number of other homologous series of ω-phenoxy acids were prepared and their plant growth-regulating activity assessed. Now on several occasions (Wain, 1951, 1953), I have stressed the importance of using a variety of tests for such assessment and indeed, in all work at Wye with new compounds, at least three methods have been used, each employing a different type of plant tissue. In this β-oxidation work (Wain & Wightman, 1954) the wheat cylinder elongation test, the pea curvature test and the tomato leaf epinasty test were used. The results obtained with several homologous series are indicated in Table 1. It can be seen that a clear alternation in biological activity, consistent with the β-oxidation hypothesis, is exhibited by most of these series in all tests. On the other hand, with the 2:4:5-series for example, we have most unexpected behaviour for although the alternation is shown in the cylinder test, all homologues higher than the acetic are inactive in the pea curvature and tomato epinasty tests.

TABLE 1. *Alternation in activity in homologous series of substituted ω-phenoxyalkylcarboxylic acids*  *in three tests*

	Test		
Ring substituents	Wheat cylinder	Pea curvature	Tomato epinasty
4-Chloro-	Yes	Yes	Yes
2:4-Dichloro-	Yes	Yes	Yes
2-Methyl-4-chloro-	Yes	Yes	Yes
3:4-Dichloro-	Yes	Yes	Yes
3-Methyl-4-chloro-	Yes	Yes	Yes
2:4:5-trichloro-	Yes	No	No
2:4-Dichloro-5-methyl-	Yes	No	No
2-Methyl-5-chloro-	Yes	No	No

Now evidence has already been presented that an alternation in activity in such series as these can be ascribed to a degradation of the side chain of the acids by β-oxidation. That β-oxidizing enzyme systems are present in all three types of plant tissue employed is indicated by the clear-cut alternation shown, for example, by the 4-chloro- series in all tests. The unexpected inactivity of the 2:4:5-trichlorophenoxy- butyric, caproic and octanoic acids then, might indicate that the β-oxidation enzymes present in pea and tomato stem tissues cannot operate when this 2:4:5-trichlorophenyl ring system is present though the enzyme system in the wheat tissue can do so.

If this is in fact the case, it should be possible to demonstrate the formation of the acetic derivative from alternate higher homologues by exposing the compounds to wheat cylinder tissue. Accordingly, solutions of all the 2:4:5-trichlorophenoxy acids were pretreated with wheat cylinders and these same solutions were then examined in the pea curvature test. The typical alternation in activity was at once apparent indicating that the enzyme system present in the wheat tissue had degraded alternate homologues to the acetic derivative, active in the pea test. That such a conversion was actually taking place was proved in the case of γ-(2:4:5-trichlorophenoxy)butyric acid. Solutions of this acid were pretreated with wheat cylinders as before, and ether extracts of the solutions applied as spots on the starting-line of a filter-paper chromatogram. Four experiments were carried out and in each case, on developing the paper, the acetic acid was found to be present. In other similar investigations, the portion of the chromatogram corresponding to the acetic acid position was cut out and placed in water with fresh pea segments. These developed a positive growth response (Wain & Wightman, 1954).

All these results then, provide further evidence for β-oxidation and indicate that, whilst different types of plant tissue may all possess such enzyme systems, whether or not they are capable of degrading the side chain of specific ω-phenoxyalkylcarboxylic acids depends on the nature and position of the nuclear substituents present.

Such considerations led me to the possibility of using certain of these butyric, caproic and octanoic derivatives for inducing growth responses in one kind of intact plant and not in another. In other words, here was a logical approach to selective weed control based upon enzyme make up. It remained to put these ideas to the test.

This season, a range of crop plants and weeds have been treated with γ-(2:4:5-trichlorophenoxy)- and other phenoxy- butyric, caproic and octanoic acids. The results leave us in no doubt that some of these compounds have a part to play in selective weed control. Furthermore, it would appear that differences in morphology and habit of growth between crop and weed upon which selective weed control with sulphuric acid, dinitro-*ortho*-cresol and copper salts is largely based, may not be such important factors with these new materials. Thus we have shown that certain horticultural crop plants, for example, celery, carrot and parsnip are but little affected by some of these compounds at doses which destroy a number of weeds frequently infesting such crops. Again, the indications are that various weeds might be eliminated from agricultural crops such as clover, lucerne and peas by means of specific compounds of this type.

Whereas the ease with which the various aryloxy acids under investigation can penetrate into and move within the tissue of crop and weed must be factors in such selective action, our results indicate that where such penetration occurs, plants whose enzyme make-up enables them to degrade the aryloxy acid to the corresponding acetic derivative are severely affected whereas other plants are not.

The principle of this new method of selective weed control is strikingly shown in the case of celery (*Apium graveolens*) and annual nettle (*Urtica urens*). When celery plants are sprayed with solutions of ω-(2:4-dichlorophenoxy)- or ω-(2-methyl-4-chlorophenoxy)alkylcarboxylic acids as their sodium salts, only those receiving the acetic acid are affected (Pl. 5). In the case of the annual nettle, however, the plants treated with the acetic, butyric and caproic acids are all rapidly affected and killed outright within 10 days, whereas the propionic, valeric and heptanoic derivatives produce no growth responses whatsoever (Pl. 6). Creeping thistle (*Cirsium arvense*) is another common weed which succumbs readily to alternate homologues of the above acetic acids, though this plant is affected to a much less extent by the corresponding 2:4:5-trichloro derivatives.

The use of 2:4-dichlorophenoxyacetic acid and 2-methyl-4-chorophenoxyacetic acid on grassland and corn undersown with clover has always been attended by the danger of destroying this valuable legume crop. For this reason a great many field experiments have been carried out to discover at what rates 2:4-D and MCPA can be safely used when clover is present. Applications as low as a few ounces per acre have been recommended, a much lower efficiency in weed destruction having to be accepted. Work at Wye has shown that some of our butyric acids, whilst controlling certain weeds, have but little effect on red and white clover. The acetic acids on the other hand applied at similar rates can produce disastrous effects on this crop.

It appears then, that a number of important crop plants do not possess an enzyme system which can bring about an efficient conversion of certain ω-phenoxy-butyric, caproic and octanoic acids to the active acetic derivative, whereas this change can be rapidly effected within the tissues of many weeds. It will be appreciated of course that these new selective weed killers have their limitations. For one thing, they will not control as wide a range of weeds as 2:4-D and MCPA. Again, they should not be expected to destroy weeds which are resistant to the corresponding acetic acid for it is on their conversion to this derivative that their activity is largely based. In this latter connexion, however, the influence of possible differences in penetrative properties should not be overlooked. It should also be noted that whereas some plant species remain unaffected and some are destroyed when treated with these compounds, other species may show intermediate effects.

One other point deserves mention in this brief review of our work. We have evidence that soil micro-organisms possess the capacity to degrade the side chain of certain of these butyric acids. It might be expected, therefore, that if such a compound is applied to the soil or washed off the plants by rain soon after application, it might be converted in the soil to the acetic acid and be absorbed as such through the roots of crop plants. So far, our experiments have indicated that with low-volume applications, little danger of crop damage arises from this cause.

In summary then, the important feature of these newer materials, amongst which I would mention in particular the 4-chloro-, 2:4-dichloro-, 2-methyl-4-chloro-, 3:4-dichloro- and 2:4:5-trichloro- derivatives of γ-phenoxybutyric acid, is that they open up new possibilities for destroying weeds in certain horticultural and agricultural crops which are themselves susceptible to other selective herbicides. It will be appreciated that much remains to be done with these materials in the field using a wide variety of crops and weeds. I hope to present more of our own results at an early date, but I have said sufficient, I think, to indicate the type of academic investigation which has led us to study these compounds. Other aspects of our β-oxidation work have not been dealt with; for example, the effect of side-chain substituents in preventing such oxidation, but as all this is in the press it can be consulted elsewhere (Wain & Wightman, 1954).

From the practical aspect, although our present evidence is limited to preliminary studies with some fifty crops and weeds, it seems certain that compounds of the type I have been discussing will find specific commercial uses in selective weed control.

In conclusion I should like to express my warmest thanks to Dr F. Wightman and Dr C. H. Fawcett both of whom have been closely connected with all aspects of this work. Thanks are also due to Dr K. Gaimster, Miss R. Pascal, Miss M. B. Pybus, Miss J. M. A. Ingram, Mr F. Taylor, Mr D. Simons, Mr P. Cozens, Miss M. Peattie and Mr R. C. Seeley for their valuable assistance during these investigations. Grateful acknowledgement is also made to the Agricultural Research Council, in whose Unit at Wye, this work was carried out.

REFERENCES

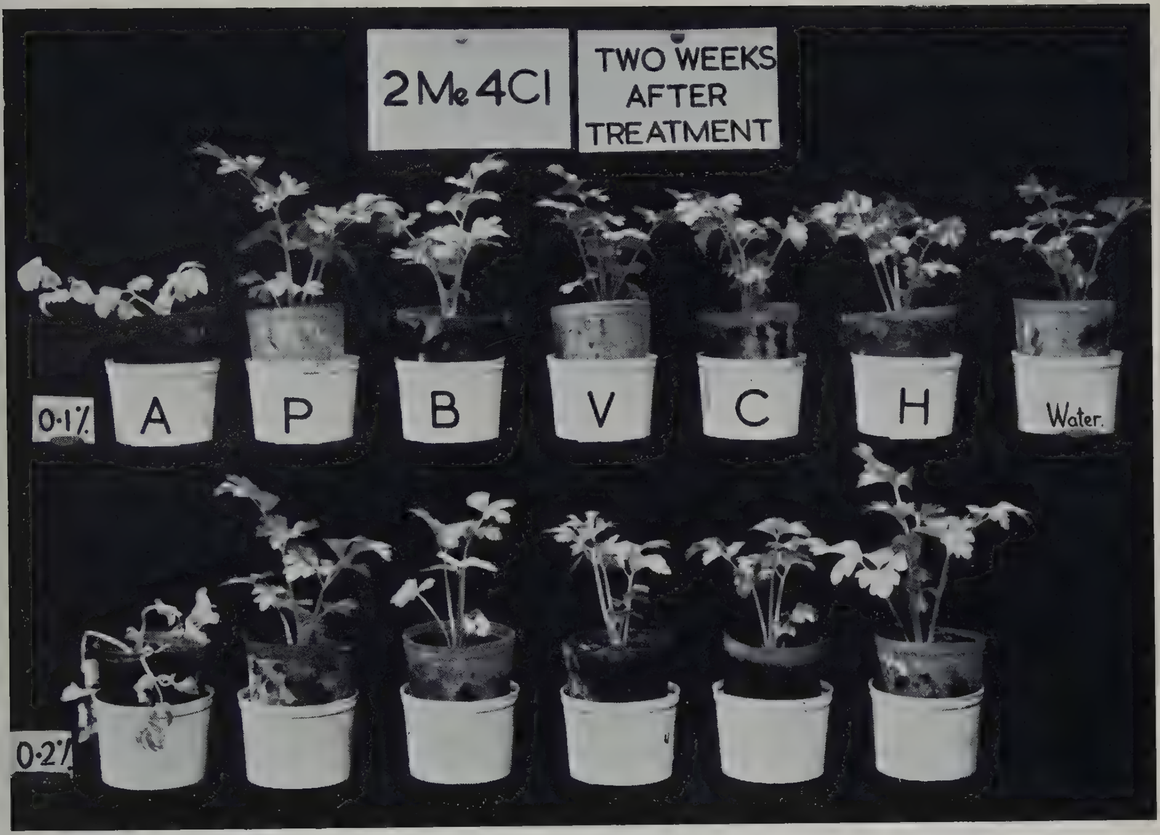
BEINERT, H. (1953). Studies on the fatty acid oxidizing system of tissues. II. β-Keto-acylderivatives of coenzyme A. *J. biol. Chem.* **205**, 575.

BREUSCH, F. L. (1948). The biochemistry of fatty acid catabolism. *Advanc, Enzymol.* **8**, 347.

FAWCETT, C. H., INGRAM, J. M. A. & WAIN, R. L. (1954). The β-oxidation of ω-phenoxy-alkylcarboxylic acids in the flax plant in relation to their plant growth-regulating activity. *Proc. Roy. Soc.* B, **142**, 60.

GRACE, N. H. (1939). Physiological activity of a series of naphthyl acids. *Canad. J. Res.* **17**, 247.

KNOOP, F. (1904). Der Abban aromatischer Fettsäuren im Tierkörper. *Beitr. chem. Physiol. Path.* **6**, 150.


2 Me 4Cl
TWO WEEKS AFTER TREATMENT
0·1%
A
P
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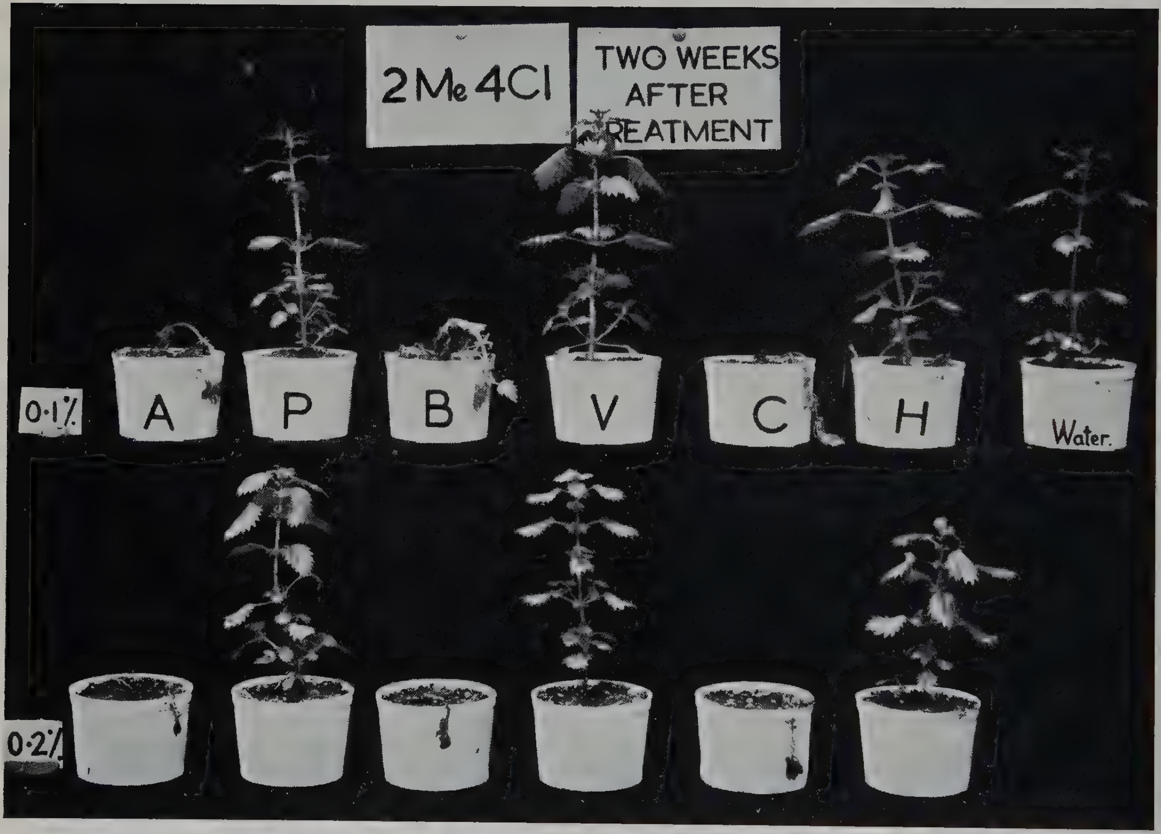
V
C
H
Water.
0·2%

WAIN—*A new approach to selective weed control*


2Me4Cl
TWO WEEKS AFTER TREATMENT
0·1%
A
P
B
V
C
H
Water.
0·2%

WAIN—*A new approach to selective weed control*

Lehninger, A. L. (1952). Enzymic oxidation of fatty acids. *Biochem. Soc. Symp.* no. 9, p. 66.

Lehninger, A. L. & Greville, G. D. (1953). The enzymic oxidation of *d*- and *l*- β-hydroxybutyrate. *Biochim. biophys. Acta*, **12**, 188.

Synerholm, M. E. & Zimmerman, P. W. (1947). Preparation of a series of ω-(2:4-dichlorophenoxy)- aliphatic acids and some related compounds with a consideration of their biochemical role as plant growth-regulators. *Contr. Boyce Thompson Inst.* **14**, 369.

Wain, R. L. (1951). Plant growth-regulating and systemic fungicidal activity. The aryloxyalkylcarboxylic acids. *J. Sci. Food Agric.* **3**, 101.

Wain, R. L. (1953). Plant growth substances. *Royal. Inst. Chem. Monograph*, no. 2.

Wain, R. L. & Wightman, F. (1954). The growth-regulating activity of certain ω-substituted alkylcarboxylic acids in relation to their β-oxidation within the plant. *Proc. Roy. Soc.* B. **142**, 525.

EXPLANATIONS OF PLATES 5 AND 6

Plate 5

Effect of ω-(2-methyl-4-chlorophenoxy)alkylcarboxylic acids on celery (*Apium graveolens*). Left to right: acetic, propionic, butyric, valeric, caproic, heptanoic derivatives and water control; top row: 0·1 % solutions: bottom row: 0·2 % solutions of the acids as sodium salts, sprayed on the plants.

Plate 6

Effect of ω-(2-methyl-4-chlorophenoxy)alkylcarboxylic acids on annual nettle (*Urtica urens*). Left to right: acetic, propionic, butyric, valeric, caproic, heptanoic derivatives and water control; top row: 0·1 % solutions; bottom row: 0·2 % solutions of the acids as sodium salts, sprayed on the plants.

Burström, Hans (1955). *Ann. appl. Biol.* **42** 158–161

ACTIVITY OF PLANT GROWTH REGULATORS

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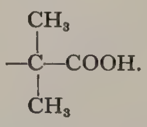
The many synthetic plant growth regulators have been divided into two groups: auxins, to which belong the common herbicides, and antiauxins, which at present are of no practical importance. There are further several chemically related compounds, which are classified as growth-inactive. The two last-mentioned groups play a certain role, however, in the current discussion of the relation between the chemical structure of the compounds and their growth activity.

According to a definition recently given by an American committee of experts, auxins are substances of a certain chemical structure able to increase the elongation of stem parts. Antiauxins, on the contrary, are substances acting as competitive inhibitors of auxins. This is a term borrowed from biochemistry, where it implies a competition between an enzyme or an activator and an inhibitor for a location in the cell, which the active compound must reach in order to exert its activity.

It is, as a matter of fact, a rather heterogeneous lot of substances which have been called antiauxins. The term is partly used to denote compounds which are in themselves inactive as growth factors, but which are able to counteract the effects of simultaneously added auxins, e.g. 2:4-D. Such antagonistic effects are found with compounds of different chemical structure, some far removed from auxins; it is at least superficially a special case of the general phenomenon of antagonism between two compounds and it is not certain or in some instances even probable that the competition takes place at the point of action of the auxin.

There are, on the other hand, also substances which in themselves are growth-active, but which exert an action judged to be the opposite to those of auxin. An outstanding position among such antiauxins is occupied by the α-substituted isobutyric acids. They differ from the corresponding auxins, the native auxin β-indoleacetic acid or the herbicides 2:4-D or 2-M:4-C, only in that the acetic acid side chain—CH_3COOH is replaced by the isobutyric acid



$$-\overset{\displaystyle CH_3}{\underset{\displaystyle CH_3}{\overset{|}{\underset{|}{C}}}}-COOH.$$

This makes the physiological difference that, whereas auxins decrease the growth of roots, this is considerably enhanced, up to two or three times, by the isobutyric acids. The herbicides are converted into root-growth-promoting substances harmless to shoots. It is assumed that they compete with the natural auxin in the plants, just as they have been shown to be able to counteract externally added auxins. They should be true antiauxins.

However, this simple view has been questioned by Rufelt at our institute, who has studied the action of these compounds on the geotropic response of roots. He has verified an old statement that there are two different geotropic reactions, one dominating positive reaction, and a weaker negative one. Of the tested growth regulators, indoleacetic acid affects the positive geotropism, but phenoxyisobutyric acid the negative response, which means that the auxin and the antiauxin are not ideal antagonists, but act upon different parts of the growth mechanism. It follows, however, from current theories of the relation between structure and activity of the growth compounds, that the isobutyric acids should be antagonists of auxins, and we have for that reason made an attempt to study more in detail the growth activity and particularly their relation to auxin. I will give a sketch of the results, which will be prefaced with a summary of the action exerted by the auxins themselves.

As mentioned, auxins are characterized by their ability to increase the cell elongation in shoots. Their physiological effect is not restricted to this action, however, but they are also able to promote cell divisions under certain conditions and in certain concentrations, for example in cambia, at the initiation of adventitious roots, and in tumours arising as a result of herbicidal effects. Furthermore, the auxins strongly inhibit the growth of roots, which is a most conspicuous property. These phenomena are well known to everyone working with auxins, theoretically or practically, and enter into the complex picture of the herbicidal action of some of them. As regards the cytological side, it has been shown repeatedly that auxin increases the tensibility of the cell wall, making it more elastic, more plastic, or both together. In one theory of cell elongation this is supposed to be a primary effect of auxin, and it is at least partly responsible for its growth activity.

If we now turn to the antiauxins of the isobutyric acid type, we should expect them to have the reverse activities of the auxins, if they were real competitors of auxin. However, this is just what we have completely failed to disclose.

To begin with the antiauxins are reported to be practically inactive on shoots; the only instance recorded in the literature of an activity is one of a weak auxin action. This is interesting because it disposes of the idea that the isobutyric acids generally antagonize auxin. It is, of course, always possible to construct a more or less complicated explanation to account for results absolutely contrary to those expected, but the most simple conclusion is that the assumption has been wrong, and that on shoots the isobutyric acids behave as auxins if anything at all.

The root elongation, on the contrary, is very much increased, which is the original reason why the compounds were classified as antiauxins. However, the very marked increase in root length may only partly depend upon an increased cell elongation and is partly due to an increased rate of cell multiplication in the apical meristem. The antiauxins always increase the cell elongation and sometimes the cell multiplication as well, but we cannot at present control the conditions necessary for an effect on the cell division activity in the meristem. It is for that reason a fairly irregular phenomenon. If this effect is very strong then the increase in the cell elongation is somewhat lowered. We are inclined to explain this by claiming that there is an upper limit for the total elongation of a root, and cell elongation and cell multiplication will to some extent compensate each other. Usually both of them increase on an addition of an isobutyric acid, and undoubtedly the increase in the rate of cell multiplication is also caused by the antiauxin.

The tensibility of the cell walls is very high in growing roots and can apparently not be increased unless there is an inhibition of the elongation as with auxin. It is possible, however, to decrease the tensibility by minute additions of growth regulators of the coumarin type. These are highly growth-active, but before there is any visible change in growth they make the cell wall wholly rigid. Treated with isobutyric acid such roots regain the normal tensibility of the cell wall. This shows that if conditions permit the tensibility of the walls to be affected by the antiauxins at all, it changes in the same direction as under the influence of an auxin.

Supplied in higher concentrations, the isobutyric acids inhibit the root elongation, just as practically all growth regulators do. This effect is usually called a toxic effect, a less specific action than the real growth activity. It is distinctly separated from the growth-increasing action; it may appear in concentrations slightly higher than the promoting one, or there may be a broad optimal range before the inhibition sets in. With the auxins, on the contrary, it is experimentally impossible to draw a borderline between the growth inhibition of roots, which is interpreted as a real auxin effect, and such an unspecific toxic action, which undoubtedly exists, particularly in the herbicides.

These general results are summarized in Table 1. If the results of the study are presented in this way, not much remains of the antiauxin activity of the isobutyric acids. We find, on the contrary, that these exert the same types of action on roots or to some extent even on shoots, as the genuine auxins on shoots, and Berit Hansen, who has carried out most of this investigation, has suggested that the isobutyric acids be regarded as auxins for roots, such a term being as justified for roots as the denotation auxin on shoots for the indoleacetic acid and 2:4-D. Whether this is more than a matter of definitions depends upon the extent to which morphologically similar actions are physiologically identical. The isobutyric acids have been called antiauxins because the auxin action under (4) has been compared with the antiauxin action under (1), but such a comparison may be wrong.

TABLE 1

Auxins (β-indoleacetic acid, 2:4-D, etc.)	Antiauxins (Homologues of iso-butyric acids)
(1) Increase the cell elongation in shoots	*idem* in roots (and shoots?)
(2) Increase the cell multiplication under certain conditions	*idem* in roots
(3) Increase the cell wall tensibility	*idem* in roots
(4) Decrease root growth	*idem* in high concentrations

The available data seem to justify the conclusion that we have in these compounds several different physiological actions. One may be the real auxin effect and the other subsidiary ones, or they may all be independent of one another. The important point is that the different effects vary quantitatively and independently between compounds and between parts of the plant.

This phenomenon is not new, but is already known from the hormonal herbicides. They are auxins, but whereas in β-indoleacetic acid the auxin effect (1) dominates, in the herbicides the actions listed under (2) and (4) and perhaps others dominate, making these compounds herbicides. On the other hand, in the isobutyric acids the action (1) on roots dominates giving them the apparent properties of antiauxins.

It seems as if the true auxins, herbicides, and antiauxins formed one group of growth-active compounds characterized by several morphological effects, to a varying degree present in all of them. The problem of the antiauxins would then be similar to or even identical with that of the herbicides. It should also be mentioned that the antiauxins show selectivity in so far as that grasses are particularly sensitive and Dicotyledons less so. This interpretation is at variance with the current theories of the relation between structure and activity of the compounds. On the other hand, elucidating the connexion between the above-mentioned morphological growth effects seems to be necessary for an explanation of both the antiauxin and the herbicidal properties of compounds of this type.

Templeman, W. G. (1955). *Ann. appl. Biol.* 42, 162–173

THE USES OF PLANT GROWTH SUBSTANCES

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(With 1 Text-Figure)

The word *hormone* was used for the first time forty-nine years ago by Starling (1905) to describe a substance active in chemical correlation in animal physiological studies. At that time the presence of similar regulators in plants was perhaps suspected, but it was not until the publications of Boysen Jensen (1910, 1911, 1913) and those of Paál (1914, 1918) that the transmission of a stimulus, in this case phototropic, could be ascribed to an active substance. This hormone was isolated by Went (1926). It remained to Kögl, Haagen-Smit & Erxleben (1934) to identify β-indolylacetic acid as an auxin. It is from this point, and from the work of Hitchcock (1935), Zimmerman & Wilcoxon (1935) on synthetic plant growth regulators published the next year, that the major developments in this field can be traced. The whole subject was well recorded and reviewed by Audus (1953).

It is becoming increasingly difficult to define a plant growth regulator. Audus (1953) used phytohormone synonymously with plant growth-regulating substance to mean 'an organic compound which, in extremely low concentrations, regulates the growth of the plant in one or more of its several aspects'. That definition will be used here provided it is recognized that the examination of a large number of substances has revealed a wide concentration range over which a particular effect may be induced. In other words a growth regulation may be brought about by compound A at one concentration and the identical effect by compound B at many times less or more than the concentration necessary of compound A. The amount of emphasis which can be placed on concentration in this definition has lessened.

Thousands of chemicals have been synthesized and tested for effectiveness on one or more aspects of growth regulation. Active compounds now find established uses for the stimulation of the rooting of cuttings, the prevention of sprouting of tubers, the induction of parthenocarpic fruit formation, prevention of preharvest fruit drop and selective weed control. In practical agricultural importance the herbicidal use far outweighs all the others. Defoliation, fruit ripening, blossom thinning and growth control as distinct from plant killing are all uses for which plant growth regulators are being examined on a commercial scale; they will not be dealt with in this paper. Attention will be restricted to established uses in horticulture and agriculture.

ROOTING OF CUTTINGS

Methods of vegetative reproduction are of great importance in raising new plants of many economically important species. Some of these depend on subjecting some detached portion of the parent plant to conditions which promote root initiation and development resulting in a new complete plant. Shoot, root and leaf cuttings are frequently used. Miscellaneous chemicals have been employed over many years to assist the rooting of cuttings but mostly only small and indefinite results were achieved. It was in this field that synthetic plant growth regulators were first adopted in commercial practice. Cooper (1935) was the first to show that β-indolylacetic acid in lanoline paste stimulated the rooting of lemon cuttings. It is interesting to note that applications were at first apical as it was thought this simulated natural auxin source and transport conditions. Basal applications were soon shown to be equally effective and considerably more convenient.

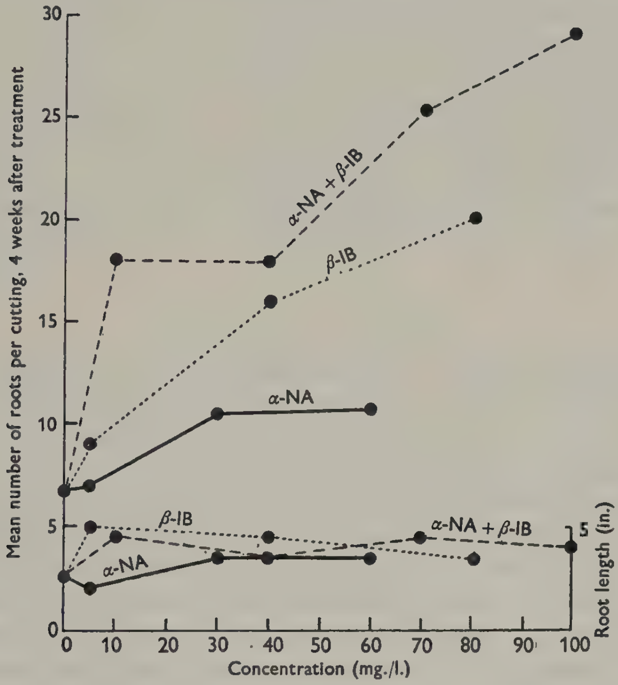

Fig. 1. Cacao cuttings: effect of growth regulators on rooting. αNA = α-naphthylacetic acid; β-IB = β-indolylbutyric acid. (From data of Evans, H., 1951, *Trop. Agric.* **28**, 147.)

In the next year or two many chemicals were examined and it was quickly established that β-indolylbutyric acid and α-naphthylacetic acid were very suitable. These two have remained the most popular since their early use, and only recently have the halogen-substituted phenoxy propionic (e.g. α-(2:4:5-trichlorophenoxy) propionic acid) and *n*-butyric acids been shown to be highly active root initiators. Type and form of rooting vary somewhat with small changes in molecular structure, and it is reasonable to expect that some specificity between compound and plant will be found.

The normal methods of treatment of the cuttings are by application of the chemical in a lanoline paste to the basal end, by standing the cuttings with their basal ends in a dilute solution for a period of several hours or by momentarily dipping the basal ends in either a concentrated solution or dust. In practice, the lanoline paste method is cumbersome and little used, and much of the commercial usage is of the concentrated liquids or dusts.

A wide range of plant species has been tested for rooting response to plant growth regulators, and for details the lists prepared by various workers (e.g. Pearse, 1948; Audus, 1953) may be consulted.

Use of these compounds is made in commercial nurseries, and cocoa and rubber are two of the most important crop plants where this method has proved particularly useful. Fig. 1 (Evans, 1951) indicates the type of results which are obtained.

INHIBITON OF BUD GROWTH

It has long been known that an active terminal bud of a shoot possesses the power of inhibiting the growth of lateral buds, and Guthrie (1938) showed that α-naphthylacetic acid as its potassium salt (and later in ester form) prevented the sprouting of potatoes in store. Methyl α-naphthylacetate has found wide use for this purpose. 2:3:5:6-tetrachloronitrobenzene (Brown, 1947) is an active sprout depressant but not so effective as isopropyl *N*-phenyl-carbamate (IPC) which applied at about 0·0027% on the tubers effectively inhibits sprouting for several months (Rakitin & Troyan, 1949; Rhodes, Sexton, Spencer & Templeman, 1950; Rhodes, Spencer, Templeman & Sexton, 1951). Isopropyl *N*-(3-chlorophenyl)carbamate is even more effective (Marth & Schultz, 1952). Unfortunately IPC also reduces the tubers' ability to develop suberized tissue to seal off invading hyphae of *Oospora pustulans* (skin spot) (Dillon Weston, 1952).

The results of an Australian experiment with IPC (Downie, 1952) are given in Table 1.

With both α-naphthylacetic and chlorinated-phenoxyacetic esters and the phenylcarbamates it is necessary to apply the active chemical as an external spray or dust to the harvested tubers. Maleic hydrazide, however, has shown marked sprout-inhibiting properties on the bulbs during storage when sprayed on to the foliage of onions several weeks *prior* to harvesting (Witwer, Sharma, Weller & Sell, 1950) and has also proved effective on potatoes (Zukel, 1950). The results so far obtained have not been as good as those obtained by direct application of the phenylcarbamates to the tubers and it remains to be seen whether an effective sprout inhibitor can be combined with an effective haulm-destroying spray so that the two requirements may be achieved by one operation.

It has been suggested that the bud-inhibiting properties of some of these plant growth regulators should be used for such purposes as delaying the bud opening of fruit trees until the danger of frost is past and for preventing sucker growth of tobacco. The results of experiments so far have not permitted recommendations being made for these purposes.

TABLE 1. *Effect of IPC on potato sprouting 5 months after treatment*

(Original weight of tubers = 10 lb. After Downie, W. A. (1952). *J. Dep. Agric. Vict.* 50, 61.)

	Control			IPC 2 % dust at 3 lb./ton tubers		
Variety	Tuber weight lost (oz.)	Weight of sprouts (oz.)	Total weight lost (%)	Tuber weight lost (oz.)	Weight of sprouts (oz.)	Total weight lost (%)
Green Mountain	24	18	26	15	0	9
Katahdin	22	23	28	13	0	8
Up-to-date	20	12	20	15	0	9
Late Carman	20	26	29	17	Tr	11
Exton	20	10	19	14	0	9
Sequoia	19	10	18	13	0	8
Mean	21	16	23	15	0	9

FRUIT PRODUCTION

Three main uses for plant growth regulators in commercial fruit production have been found: (i) for the initiation of parthenocarpic fruit production, (ii) for the prevention of the drop of immature fruit, and (iii) a specialized application for the acceleration of flowering of pineapples.

The influence of pollen extracts on fruit development has been known for many years, and now many plant growth regulators have proved capable of inducing parthenocarpic development (see Audus, 1953). Various indolyl, naphthyl and substituted phenoxyacetic acids are active, and effective applications have been made as aqueous solutions, dispersions, aerosols and vapours (of the volatile esters) to flowers at the appropriate stage of growth. There are minor differences in response (due to differences in fruit shape, nature of flesh and thickness of skin) from different compounds and some evidence that best results are obtained by using mixtures.

As in all the applications of plant growth regulators there are wide differences in the fruit production stimulated for different plant species. Tomatoes are notable in their response, but excellent results have been achieved with figs (Smyrna and Calimyrna varieties), apples, pears, plums and strawberries, and several others. This practice has shown up to advantage where pollination is difficult or seedless fruits desirable. It has been particularly valuable for the tomato under conditions where a good early fruit set is achieved only with difficulty due mainly to unfavourable seasonal variations in the weather.

As an example of the type of result which may be obtained, two experiments carried out in 1948 and reported by Wain (1950) may be quoted in Table 2.

TABLE 2. *Effect of growth regulators on fruit set*

(Total yield of tomato fruit from bottom trusses, 1948 Variety 'Harbinger'. Grown outdoors. OCP = α-(2-chlorophenoxy) propionic acid (40 p.p.m. of acid); BNA = β-naphthoxyacetic acid (60 p.p.m. of acid); BNP = α-(β′-naphthoxy) propionic acid (100 p.p.m. of acid); mixture = BNA (40 p.p.m. of acid) plus 4-chlorophenoxyacetic acid (10 p.p.m. of acid). From Wain, R. L. (1950). *J. hort. Sci.* **25**, 249.)

Treatment	Canterbury (oz. per 240 plants)	Wye (oz. per 192 plants)
OCP	2999	2889
BNA	2958	2214
BNP	3049	2501
Mixture	3643	2682
Control	2292	644
Spraying dates	1 July	29 July

All the above were used as methylglucamine salts and each spray contained 0·004% wetting agent.

It must, however, be emphasized that general American experience with tomatoes is that earliness may be promoted but total yield is little influenced by the use of hormone sprays.

The prevention of premature fruit drop by the use of growth-regulating chemicals is now widely used for various apple varieties. For over 20 years it has been thought that auxins play a part in abscission, and La Rue (1936) prevented leaf fall by the use of several synthetic compounds. In studies on parthenocarpy Gardner & Marth (1937) found that leaf and berry fall in holly could be prevented and, soon after, these workers and Batjer (1939) found that the preharvest drop of apples could be stopped. Close relationships between auxin production by the seed and the amount of fruit drop has been shown by Luckwill (1948). Low auxin content leads to abscission.

There is again varietal and species variation to growth regulator treatment but the pome and citrus fruits give best response; apples, and to a less extent pears, are the commercial crops most widely sprayed. α-Naphthylacetic acid at a spray concentration of around 10 p.p.m. is the most popular treatment but a number of other compounds over a range of concentrations are known to be effective. The chief practical difficulty is to know when to spray and this can only be calculated by prior knowledge of when a particular variety is likely to drop fruit and the average period of effectiveness of a given compound for it. Sprays are almost universally used but various dust and injection methods have been proposed as have combinations with various fungicides and insecticides.

In connexion with pineapple culture van Overbeek (1951) states that the date of harvest in Hawaii and South America can be accurately regulated by a single application of about 1 oz./acre of α-naphthylacetic acid at a total cost of about 5 U.S. dollars per acre. Pineapple varieties vary greatly in the time taken to reach the flowering stage and under natural conditions this is of somewhat spasmodic occurrence. Spraying the plants with a solution of α-naphthylacetic acid (of 5–10 p.p.m. concentration) initiates flower primordia and allows a cropping programme to be laid down. Harvesting dates can be arranged and fruit gathering can rotate around the fields of the farm.

WEED CONTROL

Until the discovery of the so-called hormone weedkillers during the Second World War the most widely used selective weedkillers were copper salts, dilute sulphuric acid and 3:5-dinitro-*o*-cresol as sprays and kainit and calcium cyanamide as dusts. With the advent of the growth regulators as herbicides the usage of non-hormone weedkillers has not diminished but has increased considerably. The scale on which the chlorinated phenoxyacetic acids are used can be estimated from available data. It is known that about 20,000 tons of 2:4-D and MCP acids were manufactured in 1952. If an average rate of application was $\frac{1}{2}$ lb./acre then the weedkillers were used on approximately 80 million acres.

Since this Jubilee meeting of this Association is attempting to review the achievements of applied biology during the last 50 years and their importance in world food production, perhaps I may be allowed to recount the sequence of British and American discoveries of growth regulators as selective weedkillers.

The discovery of the selective herbicidal action of growth regulators was made at several separate places during the Second World War and, owing to the secrecy regulations then in force, publication of the British results was very much delayed.

First, at Jealott's Hill Research Station, as a consequence of previous experiments with β-indolylacetic acid and α-naphthylacetic acid on cuttings and whole plants, it was found in the autumn of 1940 that 25 lb./acre of the latter compound killed yellow charlock (*Brassica sinapis*) without harming oats when the two were sown together and independent of whether the application was made before or after the emergence of the seedlings. Joint chemical and biological work yielded 2-methyl-4-chlorophenoxyacetic acid in 1941 and 2:4-dichlorophenoxyacetic acid in 1942; both proved effective weedkillers in cereals in pot or box scale tests at about 1 lb./acre (Sexton, Slade & Templeman, 1945; Slade, Templeman & Sexton, 1945).

Secondly, at Rothamsted resulting from work which began in 1941 (as a result of earlier work on the factors causing the curling of legume root hairs) it was found that β-indolylacetic acid and α-naphthylacetic acid were toxic to seedlings at low concentrations and, when looking for a compound with greater persistence in the soil, 2:4-dichlorophenoxyacetic acid was shown (in experiments which commenced in 1942) to be more toxic to sugar beet and red clover than to wheat (Nutman, Thornton & Quastel, 1945).

The results of the independent work at these two stations became available to each of them when the two sets of conclusions were reported to the Agricultural Research Council in November 1942. From that date onwards many field trials were undertaken by the Agricultural Research Council (Blackman, 1945; Blackman & Roberts, 1950), the Norfolk War Agricultural Executive Committee (Hudson, 1946) and Imperial Chemical Industries Ltd. (Templeman & Halliday, 1950).

Thirdly, in the U.S.A. in 1942 the chlorinated phenoxyacetic acids were reported as growth regulators, but *not* as herbicides, by Lontz (1943; Jones, 1953) and by Zimmerman and Hitchcock (1942). In a paper published in 1944 Marth & Mitchell stated that in a private communication in 1941 E. J. Kraus had suggested that plant growth regulators might be useful as herbicides. Jones (1945, 1953) has reported that he found 2:4-dichlorophenoxyacetic acid to have herbicidal properties in 1942, and in publications from the U.S.D.A. Station at Beltsville in 1944 (Mitchell & Hamner, 1944; Marth & Mitchell, 1944) 2:4-dichlorophenoxyacetic acid was shown to have *selective* herbicidal activity. There was tremendous development in research and use in the U.S.A. following these publications. When the American results appeared in print, the conclusions from the English work were also published (Slade, *et al.* 1945; Nutman *et al.* 1945; Blackman, 1945).

The principal chemicals are 2:4-dichlorophenoxyacetic acid (2:4-D), 2-methyl-4-chlorophenoxyacetic acid (MCP) and 2:4:5-trichlorophenoxyacetic acid (2:4:5-T). The latter compound was first described as a herbicide by Jones (1945, 1953) and Hamner & Tukey (1944). Especially in the U.S.A., a wide range of derivatives of these acids are in use such as sodium and alkanolamine salts and the alkyl and so-called 'low volatile' esters. Commercial products are often formulated with varying quantities of solvents, emulsifying or dispersing agents, wetters or spreaders and sometimes contain varying quantities of impurities some of which may be closely related to the active principles. It is interesting that the intensive research of the last 10 years has not produced any compounds more active in this field than the derivatives or close relatives of 2:4-D, MCP and 2:4:5-T.

By far the larger amount of these weedkillers is applied as an aqueous spray, although dusts are still used in some places. To reduce the volume of water required, so-called 'low-volume' sprayers which apply from about 5–20 gall./acre were introduced. Many of these machines are of the cheap and simple tractor-mounted type and since they were introduced for weed control purposes, uses for other plant protection agents have expanded continuously. Aerial spraying for herbicide application has also developed considerably.

The established uses for hormone weedkillers are for weed control in cereals (including maize and rice), linseed and grassland. Weed species vary widely in their susceptibility, but yellow charlock or mustard (*Sinapis arvensis*), one of the world's most widely distributed annual weeds of cereals, is very easily eradicated by 2:4-D and MCP. Since they are readily translocated they have proved particularly valuable for the control of some perennial weeds; they effectively kill water hyacinth (*Eichhornia crassipes*), one of the most pernicious floating aquatic weeds of inland waterways in warm climates. 2:4:5-T is now widely used for the control of woody plants, brush and scrub. Many weeds are dwarfed and restricted in growth by doses which eliminate susceptible species and are thus much subdued as competitors for water and nutrients, but it must be made clear that there are many weeds which are very resistant to these weedkillers.

The last decade of research on weedkillers in cereals has added much to our knowledge of the factors which influence both degree of weed control attained and any effect upon the crop. Blackman & Roberts (1950) found that an average increase in yield of grain (winter wheat, spring oats and barley) as a result of annual weed control from experiments carried out between 1943 and 1947 was of the order of 23 %. In some of the great maize-growing areas of the world this crop is very sensitive to weed competition and the value of weed control is proportionately greater.

These weedkillers are equally effective against many important weeds of pastures and rangelands but it is here more difficult to make a quantitative assessment of the benefit which accrues. The use of any increased quantities of herbage is affected by many factors and there are many deficiencies in the available experimental techniques for this type of work. An added complication is that the economics of grassland farming in many parts of the world are unfavourable to the use of any weedkiller at present prices. For these reasons only a limited amount of experimental data is available, and this is chiefly concerned with the immediate benefit in herbage yield, such, for example, as shown in the results of the following trials (Halliday & Templeman, 1951) carried out in 1946–7 (Table 3).

TABLE 3. *Control of buttercup* (Ranunculus *sp.*)

(Average yields (cwt. dry matter/acre) from eight trials. MCP applied: autumn 1946. Hay cuts: early summer 1947.)

	MCP (lb./acre)		
	0	2	4
Total useful herbage	17·6	22·8	22·4
Buttercups	8·3	2·3	1·7
Clover	2·4	1·8	0·5

Some plant growth regulators are potent mitotic poisons, and of these the phenylcarbamates have achieved most agricultural usage. Isopropyl *N*-phenyl carbamate (IPC) was found in 1941 at Jealott's Hill (Templeman & Sexton, 1945; Sexton & Templeman, 1946) to be a very potent inhibitor of germination and early seedling growth of grasses and cereals. From a series of field experiments in 1941–2 which involved about 10,000 plots, it was concluded that about 3 lb./acre of this chemical applied just before, during or within a few weeks after sowing obliterated crops of winter and spring cereals. Applications at later stages of growth if the weather conditions were suitable, arrested development and eventually killed the plants. Many broad-leaved plants were unaffected by these dressings but some dicotyledons, for example many *Polygonum* sp., chickweed (*Stellaria media*) and buckwheat (*Fagopyrum esculentum*), are sensitive.

Isopropyl *N*-(3-chlorophenyl) carbamate (Cl IPC) was found (Freed, 1949; Witman & Newton, 1951) to have greater persistence in soil than IPC and is widely used for the control of annual grasses and some other weeds in cotton when used as a pre-emergence spray. IPC itself gives effective control of wild oats (*Avena fatua*) in peas in the Pacific North-West of the U.S.A. if stirred into the seed-bed at about 4 lb./acre immediately before sowing. The figures in Table 4 show the results of one of our recent experiments.

TABLE 4. *Control of wild oats in peas*

(Deeping St Nicholas, 1954. Wild oats=plants per sq. ft.; application date: 15 April 1954; peas=plants per yard; weeds and peas counted: 18 May 1954.)

Aplication (lb./acre)		IPC		Chloro-IPC	
		Wild oats	Peas	Wild oats	Peas
0	To soil surface after sowing	35·4	23·3	35·4	23·3
4		23·5	22·9	40·7	21·1
8		28·8	22·6	19·4	23·8
12		28·8	21·4	26·9	21·6
0	Worked into seed-bed prior to sowing	49·2	23·7	49·2	23·7
4		10·8	21·8	7·6	21·1
8		7·0	22·1	4·9	22·8
12		5·3	23·4	1·7	27·1

The phenylcarbamates have not proved effective for the control of established perennial grasses. It remains to be seen whether 3-(4′-chlorophenyl) 1:1-dimethyl urea (Bucha & Todd, 1951) or some near relatives of α:α-dichloropropionic acid (Dow Chemical Co. 1953), which are also potent weedkillers, will be suitable for this purpose.

It is clear that a wide field for the use of chemicals for the control of growth and development of plants lies ahead. Even in the restricted field of weed control much will be accomplished in the next 10 years, and an example may be cited in which some novel compounds indicate yet another approach to new herbicides.

Several groups of compounds are known which, like *N*-(α-naphthyl)phthalamic acid (Mentzer & Nétien, 1950; Jones, Metcalfe & Sexton, 1954*a*), prevent seedlings responding to gravity and light in the normal way (Jones *et al.* 1954*b*, 1954*c*). When seedlings germinate in soil containing these compounds roots and shoots grow in random directions. It seemed likely that such compounds might be effective pre-emergence weedkillers and Table 5 shows the results of a field trial carried out in 1952.

Unfortunately crop growth was markedly affected and these chemicals are not suitable as selective weedkillers. Further investigation of this antitropic effect may, however, yield academically interesting conclusions with perhaps practical applications.

TABLE 5. *Pre-emergence weed control trial*

(Jealott's Hill. Treatment application: 16 April 1952; weed counts: 18 June 1952.)

Treatment	Rate (lb./acre)	Chickweed (*Stellaria media*) (plants/sq. ft.)	Groundsel (*Senecio vulgaris*) (plants/sq. ft.)
Control	—	4·4	2·8
2:4:6-tribromo-phenyl-nitramine	10	0·1	0·7
	15	0·0	0·3
2-chloro-9-fluorenol-9-carboxylic acid	5	0·1	0·3
	10	0·0	0·0

REFERENCES

AUDUS, L. J. (1953). *Plant growth substances*. London: Leonard Hill.

BLACKMAN, G. E. (1945). A comparison of certain plant-growth substances with other selective herbicides. *Nature, Lond.*, **155**, 500.

BLACKMAN, G. E. & ROBERTS, H. A. (1950). Studies in selective weed control. I. The control of annual weeds in winter wheat. II. The control of annual weeds in spring cereals. *J. agric. Sci.* **40**, 62, 70.

BOYSEN JENSEN, P. (1910). Über die Leitung des phototropischen Reizes in *Avena*-keimpflanzen. (Vorläufige Mitteilung). *Ber. dtsch. bot. Ges.* **28**, 118.

BOYSEN JENSEN, P. (1911). La transmission de l'irritation phototropique dans l'*Avena*. *Overs. danske Vidensk. Selsk. Forh.* no. 1 (Part II. Communications), 3.

BOYSEN JENSEN, P. (1913). Über die Leitung des phototropischen Reizes in der *Avena*-koleoptile. *Ber. dtsch. bot. Ges.* **31**, 559.

BROWN, W. (1947). Experiments on the effect of chlorinated nitrobenzenes on the sprouting of potato tubers. *Ann. appl. Biol.* **34**, 422.

BUCHA, H. C. & TODD, C. W. (1951). 3-(*p*-Chlorophenyl)-1,1-dimethylurea—a new herbicide. *Science*, **114**, 493.

COOPER, W. C. (1953). Hormones in relation to root formation on stem cuttings. *Plant Physiol.* **10**, 789.

DILLON WESTON, W. A. R. (1952). Private communication.

DOW CHEMICAL COMPANY (1953). *Delapon Bull.* no. 1, May.

DOWNIE, W. A. (1952). Maintenance of quality in stored table potatoes. *J. Dep. Agric. Vict.* **50**, 61, 76.

EVANS, H. (1951). Investigations on the propagation of cacao. *Trop. Agriculture, Trin.*, **28**, 147.

FREED, V. H. (1949). A comparison of toxicity of some unsubstituted aryl carbamic alkyl esters. *Proc. 11th W. Weed Conf.* p. 41.

GARDNER, F. E. & MARTH, P. C. (1937). Parthenocarpic fruits induced by spraying with growth promoting compounds. *Bot. Gaz.* **99**, 184.

GARDNER, F. E., MARTH, P. C. & BATJER, L. P. (1939). Spraying with plant growth substances to prevent apple fruit dropping. *Science*, **90**, 208.

GUTHRIE, J. D. (1938). Effect of ethylene thiocyanohydrin, ethyl carbylamine, and indoleacetic acid on the sprouting of potato tubers. *Contr. Boyce Thompson Inst.* **9**, 265.

HALLIDAY, D. J. & TEMPLEMAN, W. G. (1951). Field experiments in selective weed control by plant-growth regulators. III. Weed control in grassland. *Emp. J. exp. Agric.* **19**, 33.

HAMNER, C. L. & TUKEY, H. B. (1944). The herbicidal action of 2:4-dichlorophenoxyacetic and 2:4:5-trichlorophenoxyacetic acid on bindweed. *Science*, **100**, 154.

HITCHCOCK, A. E. (1935). Indole-3-*n*-propionic acid as a growth hormone and the quantitative measurement of plant response. *Contr. Boyce Thompson Inst.* **7**, 87.

HUDSON, H. G. (1946). Weed control in Norfolk. A new method. *Agriculture, Lond.*, **53**, 22.

JONES, F. D. (1945). U.S. Pat. Spec. 2,390,941.

JONES, F. D. (1953). Priority claims on 2:4-D. *J. agric. Fd Chem.* **1**, 912.

JONES, R. L., METCALFE, T. P. & SEXTON, W. A. (1954*a*). The relationship between the constitution and the effect of chemical compounds on plant growth. IV. Derivatives and analogues of 2-benzoylbenzoic acid. *J. Sci. Fd Agric.* **5**, 32.

JONES, R. L., METCALFE, T. P. & SEXTON, W. A. (1954*b*). The relationship between the constitution and the effect of chemical compounds on plant growth. V. Aromatic nitro-compounds and nitramines. *J. Sci. Fd Agric.* **5**, 38.

JONES, R. L., METCALFE, T. P. & SEXTON, W. A. (1954*c*). The relationship between the constitution and the effect of chemical compounds on plant growth. VI. Some derivatives of fluorene. *J. Sci. Fd Agric.* **5**, 44.

KÖGL, F., HAAGEN-SMIT, A. J. & ERXLEBEN, H. (1934). Über ein neues Auxin ('Hetero-auxin') aus Harn. XI Mitteilung über pflanzliche Wachstumsstoffe. *Hoppe-Seyl. Z.* **228**, 90.

LA RUE, C. D. (1936). The effect of auxin on the abscission of petioles. *Proc. nat. Acad. Sci., Wash.* **22**, 254.

LONTZ, J. F. (1943). U.S. Pat. Spec. 2,322,761 (reissue no. 23,115).

LUCKWILL, L. C. (1948). The hormone content of the seed in relation to endosperm development and fruit drop in the apple. *J. hort. Sci.* **24**, 32.

MARTH, P. C. & MITCHELL, J. W. (1944). 2:4-Dichlorophenoxyacetic acid as a differential herbicide. *Bot. Gaz.* **106**, 224.

MARTH, P. C. & SCHULTZ, E. S. (1952). A new sprout inhibitor for potato tubers. *Amer. Potato J.* **29**, 268.

MENTZER, C. & NÉTIEN, G. (1950). Sur un procédé permettant de troubler le géotropisme des racines. *Bull. mens. Soc. linn. Lyon*, **19**, 102.

MITCHELL, J. W. & HAMNER, C. L. (1944). Polyethylene glycols as carriers for growth-regulating substances. *Bot. Gaz.* **105**, 474.

NUTMAN, P. S., THORNTON, H. G. & QUASTEL, J. H. (1945). Inhibition of plant growth by 2:4-dichlorophenoxyacetic acid and other plant-growth substances. *Nature, Lond.*, **155**, 498.

PAÁL, Á. (1914). Über phototropische Reizleitungen. (Vorläufige Mitteilung). *Ber. dtsch. bot. Ges.* **32**, 499.

PAÁL, Á. (1918). Über phototropische Reizleitung. *Jb. wiss. Bot.* **58**, 406.

PEARSE, H. L. (1948). Growth substances and their practical importance in horticulture. *Tech. Commun. Bur. Hort., E. Malling*, no. 20.

RAKITIN, Y. V. & TROYAN, A. V. (1949). Retardation of sprouting of potato tubers by chemical substances. *C.R. Acad. Sci. U.R.S.S.*, **66**, 483.

RHODES, A., SEXTON, W. A., SPENCER, L. G. & TEMPLEMAN, W. G. (1950). Use of isopropylphenylcarbamate to reduce sprouting of potato tubers during storage. *Research, Lond.*, **3**, 189.

RHODES, A., SPENCER, L. G., TEMPLEMAN, W. G. & SEXTON, W. A. (1951). Brit. Pat. Spec. 657,512.

SEXTON, W. A., SLADE, R. E. & TEMPLEMAN, W. G. (1945). Brit. Pat. Spec. 573,929.

SEXTON, W. A. & TEMPLEMAN, W. G. (1946). Brit. Pat. Spec. 574,995.

Slade, R. E., Templeman, W. G. & Sexton, W. A. (1945). Differential effect of plant-growth substances on plant species. *Nature, Lond.*, **155**, 497.

Starling, E. H. (1905). The Croonian lectures on the chemical correlation of the functions of the body. I. The chemical control of the functions of the body. *Lancet*, 5 August (4275), p. 339.

Templeman, W. G. & Halliday, D. J. (1950). Field experiments in selective weed control by plant-growth regulators. I. Weed control in cereal crops. *Emp. J. exp. Agric.* **18**, 19.

Templeman, W. G. & Sexton, W. A. (1945). Effect of some arylcarbamic esters and related compounds upon cereals and other plant species. *Nature, Lond.*, **156**, 630.

van Overbeek, J. (1951). Use of growth substances in tropical agriculture. *Plant growth substances*, p. 225, (ed. F. Skoog), University Wisconsin Press.

Wain, R. L. (1950). Studies on plant growth-regulating substances. I. Field trials using various synthetic compounds for the setting of outdoor tomatoes. *J. hort. Sci.* **25**, 249.

Went, F. W. (1926). On growth-accelerating substances in the coleoptile of *Avena sativa*. *Proc. Acad. Sci. Amst.* **30**, 10.

Witman, E. D. & Newton, W. F. (1951). Chloro IPC—a new herbicide. *Proc. 5th N.E. Weed Control Conf.* p. 45.

Witwer, S. H., Sharma, R. C., Weller, L. E. & Sell, H. M. (1950). The effect of pre-harvest foliage sprays of certain growth regulators on sprout inhibition and storage quality of carrots and onions. *Plant Physiol.* **25**, 539.

Zimmerman, P. W. & Hitchcock, A. E. (1942). Substituted phenoxy and benzoic acid growth substances and the relation of structure to physiological activity. *Contr. Boyce Thompson Inst.* **12**, 321.

Zimmerman, P. W. & Wilcoxon, F. (1935). Several chemical growth substances which cause initiation of roots and other responses in plants. *Contr. Boyce Thompson Inst.* **7**, 209.

Zukel, J. W. (1950). Use of maleic hydrazide as a plant growth inhibitor. *Agric. Chemic.* **5**, (5), 35.

N.B. Where patent references are given the date shown is, for British specifications, the date of acceptance or publication and for U.S. specifications the date of issue; the dates of application are, of course, earlier.

AUDUS, L. J. & SYMONDS, K. V. (1955). *Ann. appl. Biol.* **42**, 174–182

FURTHER STUDIES ON THE BREAKDOWN OF 2:4-DICHLOROPHENOXYACETIC ACID BY A SOIL BACTERIUM

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(With 4 Text-figures)

Bacterial growth rates and the kinetics of detoxication have been followed during the course of breakdown of 2:4-dichlorophenoxyacetic acid in a liquid mineral salt medium by cultures of *Bacterium globiforme* isolated from garden soil. It was found that toxicity persisted apparently unchanged long after bacterial growth had ceased, and finally disappeared suddenly after a lag period comparable in duration with those obtained in soil perfusion experiments. These results can best be explained by the production of highly phytotoxic intermediates in the first stages of 2:4-D breakdown. Preliminary experiments involving paper partition chromatography indicate that there may be at least two such intermediates.

INTRODUCTION

Previous investigations on the breakdown of 2:4-dichlorophenoxyacetic acid (2:4-D) and other hormone herbicides of similar molecular structure in soil using the perfusion technique of Lees & Quastel (1946) have demonstrated clearly that the kinetics of the breakdown and its sensitivity to bacterial poisons indicate an attack on the molecule by an adapted soil micro-organism (Audus, 1949). From 'enriched' soils such an organism has been isolated on a mineral salt-2:4-D-agar medium in which the herbicide was the only source of organic carbon (Audus, 1950). The organism was shown to belong to the *B. globiforme* group. Continued subculturing on this solid medium results in a steady loss of vigour. Growth also takes place in a mineral salt solution (Thornton's solution) containing 2:4-D, if it is vigorously aerated; then there is no apparent loss of vigour. By continued subculturing into this liquid medium, with an occasional short period on agar, the organism has been kept growing and capable of decomposing 2:4-D for a period of about 4 years.

Growth, however, is never vigorous and all attempts to improve it by the addition to the culture medium of various accessory growth factors (i.e. yeast extract, casein hydrolysate, Menaphthone*, vitamin B_{12} and soil extracts) have met with little success. Growth on standard nutrient media is always luxuriant but the organism becomes immediately de-adapted. There seemed therefore little immediate prospect of cultivating the adapted organism in quantity for studies of 2:4-D breakdown in bulk. It was therefore decided to follow growth of the bacterium in the mineral salt—2:4-D solution and to observe simultaneously toxicity changes in the medium as a first step towards elucidation of the mechanism of breakdown in liquid culture.

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* 2-Methyl-1:4-naphthaquinone.

GROWTH AND TOXICITY CHANGES

(1) *Methods*

The culture medium has been a simple inorganic salt solution (Thornton's solution) containing the ammonium salt of 2:4-D at concentrations of either 0·1 % or 0·01 %. of acid equivalent. Thornton's solution has the following constitution: $(NH_4)H_2PO_4$, 0·1 %; KCl, 0·02 %; $MgSP_4$, 0·02 %. 25 ml. of this medium were placed in 100 ml. boiling tubes, sterilized and innoculated with 0·1 ml. of suspension of the adapted form of *B. globiforme* from previous liquid cultures. The cultures were then incubated at 25° C. in the dark and air from activated carbon filters was blown continuously through them. At suitable intervals (usually every 24 hr.) small samples (0·8 ml.) of the culture fluid and suspended bacteria were removed under sterile conditions and total cell counts made on a portion of the sample. A small quantity of methylene blue was added to 0·5 ml. of the suspension, and the bacteria allowed to take up the strain for at least ½ hr. This allowed easy counting in a haemacytometer. Total cell numbers were estimated per 25 ml. of the original culture.

Another aliquot (0·2 ml.) of the sample was also taken, sterilized by heating on a boiling water-bath for ½ hr. and then tested for phototoxicity by the cress root-growth test used in the previous perfusion work (Audus, 1951).

In this way a complete record was kept of the growth of bacterial numbers and changes in the toxicity of the medium for considerable periods under pure culture conditions.

Results

Fig. 1 shows the results of an experiment in which were studied two concentrations of 2:4-D (0·1 and 0·01 %). Two controls were also studied, i.e. one without 2:4-D and the other without mineral salts. Both these controls showed very little growth over the experimental period. There seems little doubt from this that the considerable growth in the presence of 2:4-D is due to the utilization of this compound as a source either of carbon or of energy for atmospheric carbon fixation.

Comparison of the growth curves in the two 2:4-D concentrations shows that the initial bacterial growth rate is independent of the herbicide concentration, but that growth ceases after about 3 days in the low concentration and continues up to about 15 days in the high concentration, although at a much slower rate. The maximum number of cells produced when growth ceases is approximately proportional to the initial concentration of 2:4-D in the medium, which is strong support for the contention that 2:4-D is being directly utilized as a fuel or carbon source.

However, toxicity changes present a less clear picture. Thus in the low 2:4-D concentration there was little significant change in toxicity detectable by the cress root test for the first 9 days, i.e. for 6 days after bacterial growth had apparently ceased; then suddenly all toxicity disappeared within 24 hr. This is the type of detoxication sequence observed in the soil perfusion experiments but there is no close correlation, as would have been expected, with bacterial proliferation. In the higher concentration (0·1 %) there was no significant change in toxicity during the phase of bacterial proliferation (0–16 days), but when growth had ceased a slow drop in toxicity became apparent and continued until the experiment was stopped after 40 days.

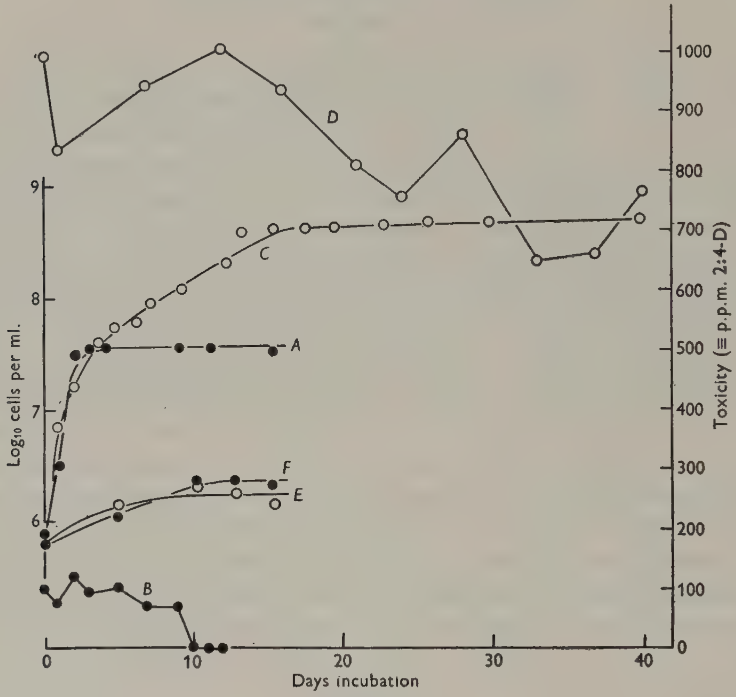

Fig. 1. Bacterial growth and 2:4-D detoxication curves for cultures of *B. globiforme* growing in a mineral salt solution containing two concentrations of 2:4-D. *A*, growth in 0·01 % 2:4-D; *B*, detoxication curve for 0·01 % 2:4-D; *C*, growth in 0·1 % 2:4-D; *D*, detoxication curve for 0·1 % 2:4-D; *E*, control growth with no mineral salts; *F*, control growth with no 2:4-D.

These results are susceptible of two explanations. The first, which we can dismiss as unlikely, is that the organism is growing on a non-phytotoxic impurity in the 2:4-D, the consumption of which does not affect the toxicity levels. Adaptation to 2:4-D breakdown then takes place over the observed lag periods (i.e. about 4 days in 0·01 % and about 16 days in 0·1 %). It would seem probable, from the relatively smooth form of the growth curves, that this adaptation takes place in non-growing bacteria. These explanations seem unlikely, since the 2:4-D used was a specially pure sample. Any impurities could not have been present in sufficient amounts to give the not inconsiderable growth of Fig. 1.

The second and, it is felt, more plausible explanation is that the initial immediate growth is at the expense of the 2:4-D itself and that the absence of any marked change of toxicity during growth is due to the fact that the initial products of the attack on the 2:4-D molecule is an intermediate with a closely similar toxicity. The subsequent lag period before detoxication would then be the phase during which the cell is building up an adaptive enzyme system capable of attacking this intermediate. As we shall see later, especially in the high concentrations, large quantities of the herbicide may remain in the culture solution after the bacteria have stopped growing. It seems unlikely that this stoppage of growth is a direct effect of too high a concentration of the substrate (2:4-D), since initial growth rates are the same in both high and low concentrations. It could best be explained by postulating bacterial growth inhibitions due to the phytotoxic intermediate produced in the 2:4-D breakdown. These results suggest that the adaptation to 2:4-D is a very rapid process, both in pure culture and in the soil, and that the long lag periods observed before toxicity disappears is the period of adaptation to the phytotoxic intermediate of 2:4-D breakdown. The toxicity of both the treated soils and of the liquid culture medium over this period would then be due to a changing mixture of 2:4-D and this breakdown intermediate.

Variants of this experiment have been performed and throw further light on this somewhat puzzling problem. Thus in the experiment illustrated in Fig. 2 two parallel cultures were set up in 0·01 % 2:4-D. When growth had stopped after 5 days a further charge of 2:4-D was added to one culture, thus doubling the amount of this compound in the medium. A rapid increase in cell numbers was observed but growth stopped after about 24 hr. A further addition of 2:4-D after 10 days, before rapid detoxication had set in, gave a further similar increase in bacterial numbers. The interesting feature of this experiment is that the rapid disappearance of toxicity took place in both cultures at the same time, starting about 12 days after the commencement of incubation. Thus further additions of 2:4-D during the process of adaptation to the intermediate do not seem, with the concentrations used, to affect the course of the adaptation.

If, however, additional 2:4-D is not added to the culture medium until after detoxication is completed then quite a different picture is obtained. Thus, in the experiment of Fig. 3, a culture, started with 'adapted' organisms on a concentration of 0·01 % 2:4-D, completed its initial growth in just over 2 days. Detoxication commenced between the seventh and eighth days and was complete in between 9 and 10 days. On the fourteenth day a further quantity of 2:4-D was supplied to bring the concentration up to the original level of 0·01 %. There was a subsequent small but significant increase in bacterial numbers. The toxicity, which was re-established on this further addition of 2:4-D, remained uncharged, however, for a further lag period of 4 days (cf. initial 7 to 8-day lag) before detoxication started. It was complete within a further 2 days.

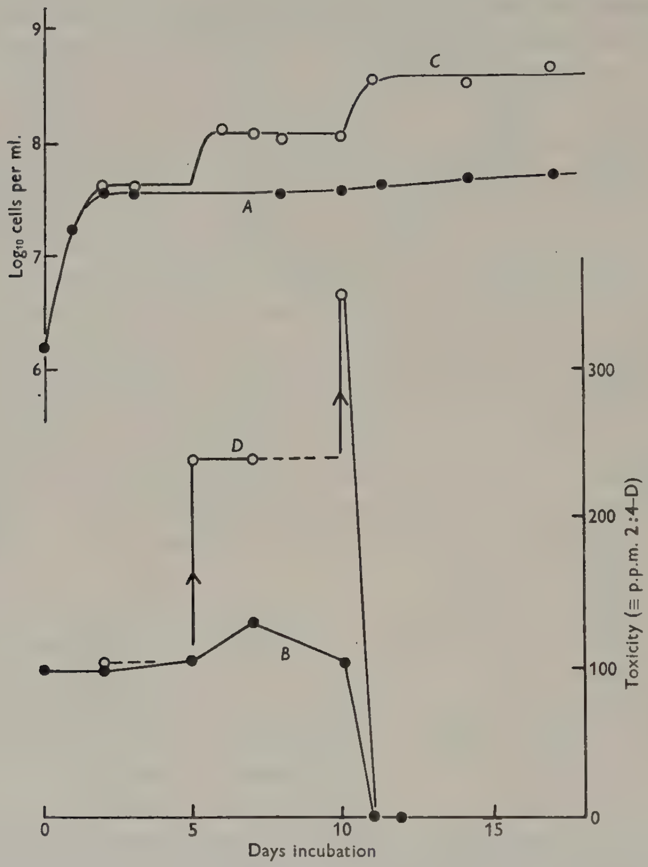

Fig. 2. Bacterial growth and 2:4-D detoxication curves for cultures of *B. globiforme* growing in a mineral salt solution containing 2:4-D. *A*, Growth curve corresponding to culture medium *B* receiving one charge of 2:4-D at the commencement of the experiment; *C*, growth curve corresponding to culture medium *D*, in which 2:4-D concentration was augmented twice before detoxication set in.

The appearance of this second lag after a first detoxication in pure culture is very surprising, since it does not happen in soil perfusion experiments. There, when a soil population has once become adapted to the breakdown of 2:4-D, this adaptation may be retained in the soil for very considerable periods of weeks or months, although it may eventually disappear (unpublished results). The differences may be due to breakdown in soil being caused by a complex population of more than one type of organism of which *B. globiforme* is only one component. The maintenance of adaptation in the soil may be a property of one of the other bacterial components not yet isolated.

Whatever the situation in soil, one possible explanation of these liquid culture results is that the enzyme system of *B. globiforme* adapted to the breakdown of the intermediate is unstable in the absence of its substrate, rapidly disappears after detoxication, and has to be re-formed when more intermediate arrives from the breakdown of 2:4-D.

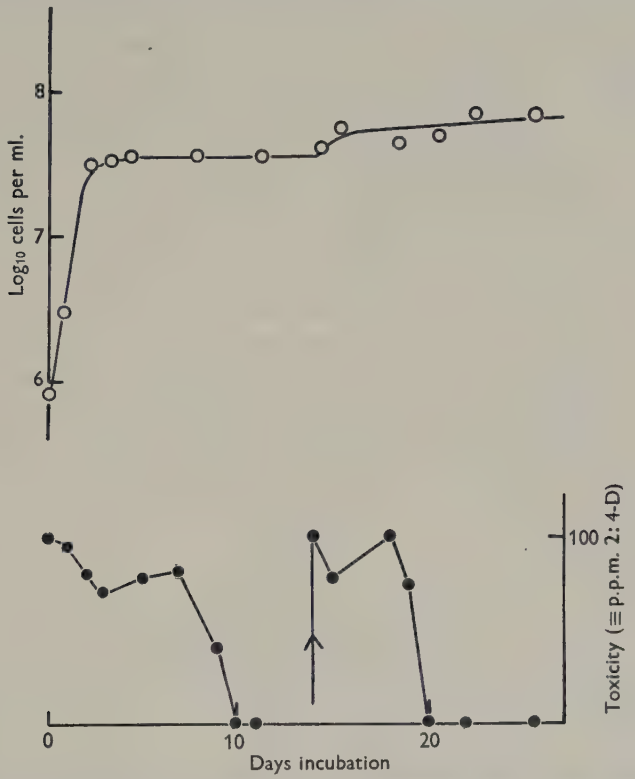

Fig. 3. Bacterial growth and 2:4-D detoxication curves for cultures of *B. globiforme* growing in a mineral salt solution containing 2:4-D, where a second quantity of 2:4-D was added to the culture medium after the first complete detoxication.

This explanation of toxicity changes during growth in pure culture calls for direct experiments to isolate and identify this hypothetical, highly phytotoxic intermediate. Attempts have been made to do so by using the methods of paper partition chromatography.

CHROMATOGRAPHIC EXPERIMENTS

One major experiment has been performed using 750 ml. of a 0·1% 2:4-D culture medium containing the usual mineral salts. This solution was sterilized and then innoculated with 15 ml. of bacterial suspension from a previous growth experiment. The suspension contained about 30 million cells per ml. It was subsequently incubated in the dark at 25° C. and vigorously aerated by blowing air through it. Bacterial growth and toxicity were measured as before and results similar to those obtained in Fig. 1 were obtained. After 40 days incubation, when toxicity of the medium still showed little change, the culture solution was acidified by the addition of about 10 ml. of conc. HCl. It was then extracted by successive shakings with ether. The combined ether extracts were then evaporated to dryness in partial vacuum until a brown crystalline residue remained. It was found that this residue consisted of at least two components, one easily soluble in warm 30% ethanol (presumably unchanged 2:4-D) while a very small fraction, a brown crystalline component, was insoluble. Separation was carried out by allowing the hot solution in 30% ethanol to cool. The brown material first separating out was filtered off and air dried. It weighed 0·3 mg., equivalent to 0·04% of the total amount of 2:4-D present in the original culture. This residue was dissolved in a small quantity of concentrated ammonia solution, the excess ammonia boiled off and a standard solution of 0·01% by weight made up. From this a series of dilutions were prepared and a cress root toxicity test carried out. It was found that the brown residue had a toxicity at least as great and possibly greater than that of 2:4-D itself.

0·5 ml. of the 0·01% solution was then placed as a spot on the starting line of a one-way paper partition chromatogram using Whatman No. 2 paper. A similar spot of 0·01% 2:4-D solution was placed on a similar strip in the same tank. After suitable equilibrium precautions the chromatograms were run using propanol–ammonia–water solvent. The papers were subsequently dried, cut into transverse strips and assayed using the pea root section technique (Audus & Thresh, 1953). The results of the assay are shown in Fig. 4 where the growth of test root sections, as a percentage of the growth of control sections on untreated filter-paper, is plotted against R_F.

It will be seen that under these conditions 2:4-D runs with an R_F of about 0·75 and that it gives a very sharp spot.* No other growth response reaching significance level is seen on the chromatogram. With the unknown inhibitor, however, three probable spots are seen. First, there is one at R_F 0·75 corresponding to 2:4-D and indicating that approximately half of the brown material was unchanged 2:4-D. Then there is another marked inhibition at R_F 0·85. This is in advance of the

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* In running 2:4-D on a chromatogram for this biological assay amounts much greater than this (i.e. 50 μg.) are not advisable. Such high amounts give complete inhibition at the centre of the spot and even the slightest tail (a fraction of a percent of the total) may give a high inhibition and thus a very broad spot.

2:4-D spot and therefore could not be explained by tailing. There can be little doubt that this is a phytotoxic compound quite distinct from 2:4-D. There is a third spot retained on the starting line and this again is taken to be a toxic compound distinct from 2:4-D. It might be suggested that this last spot is due to 2:4-D prevented from moving on the paper by some binding material extracted by the ether from the bacterial cell. This is most unlikely, since extracts of cultures made in the first few days of incubation do not show such a spot.

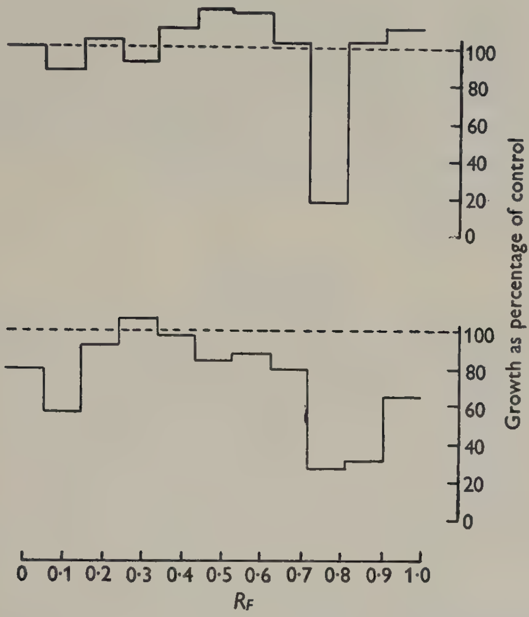

Fig. 4. Paper chromatograms of 2:4-D (top) and of the unknown substance (bottom) obtained from 40-day-old cultures of *B. globiforme* grown on a mineral salt solution containing 0·1 % of 2:4-D.

We are faced with the possibility of at least two phytotoxic intermediates in 2:4-D breakdown, and the next step is to attempt their identification and to study the kinetics of their production. Some preliminary observations of the latter have already been made by running small samples (0·5 ml.) of culture fluid from the standard experimen (25 ml. of culture medium at a concentration of 0·01 % 2:4-D) at intervals on similar chromatograms. Results so far are incomplete but they indicate that at this lower concentration both intermediates accumulate slowly at the expense of 2:4-D over the whole of the lag phase and then disappear rapidly during the short detoxication period.

It is very probable that the disappearance of phytotoxicity does not mark the complete breakdown of the 2:4-D molecule, presumably by oxidation to CO_2, water and ionic chlorine. The detection and identification of these smaller intermediate fragments of the breakdown must rely on other sensitive non-biological methods. Such methods are at present being developed. An indication of the persistence of such compounds is given by the chromatropic acid test (Freed, 1948). This test is extremely sensitive and can detect quantities of 2:4-D of the order of 0·1 μg./ml.; but it is not specific to 2:4-D, being given by a wide range of other organic compounds of similar constitution. But culture solutions which have been completely detoxicated have been shown to give a definite colour reaction with this test, pointing to the persistence of non-toxic products.

In conclusion it should be stressed that these results are very largely preliminary, and the theories to explain them have been put forward more as working hypotheses than as established beliefs. They do suggest, however, that the picture previously depicted of the course of 2:4-D breakdown in soil and the implications of cross-perfusion experiments with its homologues will have to be reconsidered in the light of these new findings.

REFERENCES

AUDUS, L. J. (1949). The biological detoxication of 2,4-dichlorophenoxyacetic acid in soil. *Plant & Soil*, **2**, 31.

AUDUS, L. J. (1950). Biological detoxication of 2,4-dichlorophenoxyacetic acid in soils. Isolation of an effective organism. *Nature, Lond.*, **166**, 356.

AUDUS, L. J. (1951). The biological detoxication of hormone herbicides in soil. *Plant & Soil*, **3**, 170.

AUDUS, L. J. & THRESH, R. (1953). A method of plant growth substance assay for use in paper partition chromatography. *Physiol. Plant.* **6**, 451.

FREED, V. H. (1948). Qualitative reaction for 2,4-dichlorophenoxyacetic acid. *Science*, **107**, 98.

LEES, H. & QUASTEL, J. H. (1946). Biochemistry of nitrification in soils. Kinetics of, and the effects of poisons on, soil nitrification as studied by a soil perfusion technique. *Biochem. J.* **40**, 803.

Problems in applied zoology

CARMICHAEL, J. (1955). *Ann. appl. Biol.* **42**, 185–189

INSECTS OF VETERINARY IMPORTANCE AND COLONIAL DEVELOPMENT

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The efficient and economic development of many of the tropical Colonial territories, especially in Africa, depends to a large extent on the control of disease, whether it be in man, animals or plants, and it is in the warmer parts of the world that insects are in this respect of major importance, because they are responsible for the transmission of many diseases which directly affect the development of the territory concerned. In this paper we are concerned with insects of veterinary importance, that is insects which primarily feed on and perhaps transmit diseases to the domestic animals, though many species are common to both animals and man, e.g. the tsetse flies, mosquitoes and ticks.

Insects do harm directly by feeding on the blood of their hosts causing anaemia and loss of condition. Further, many of them cause grave harm due mainly to worry caused by the bite leading to restlessness and loss of feeding time and subsequent unthriftiness and even death. For example in some areas of Uganda cattle cannot thrive because of the presence of large numbers of *Stomoxys* and mosquitoes even though no specific disease exists.

The most important insects, however, are those which transmit disease to cattle and other domestic animals and it is proposed to discuss some of these as they occur in the tropical Colonial territories in Africa. Of these disease transmitters the ticks and the tsetse flies are by far the most important and my remarks will be mainly concerned with these insects. Both these groups constitute a serious menace to the breeding and husbandry of domestic stock in many countries and are an important limiting factor to satisfactory agricultural and general development. Apart from the provision of meat and other animal products so essential to the nutrition of the people in the Colonial territories, it is true to say that unless domestic stock, especially cattle, can be kept the people themselves will not remain in an area. Domestic stock still has a significance to the African which cannot be measured in economic terms. Healthy cattle and other domestic stock are therefore essential to the satisfactory development of many Colonial territories, especially in Africa. Control measures are in operation and in some cases well advanced but an intimate knowledge of the life history and ecology of the various insect pests is essential before control can become efficient.

THE TICKS

This is a large group of ectoparasites belonging to the Ixodoidea which depend for their existence on animal hosts from which they suck blood. The hard-bodied ticks belonging to the family Ixodidae are the most important not only because they attach themselves to the host and suck blood but also because of the diseases they transmit. Some of the more important diseases transmitted by ticks are given in the following table:

Host	Disease	Parasite	Transmitter
Cattle	East Coast fever	*Theileria parva*	*Rhipicephalus* sp.
Cattle	Theileriasis	*T. dispar*	*Hyalomma* sp.
Cattle	Anaplasmosis or Gallsickness	*Anaplasma* sp.	*Boophilus* sp. *Rhipicephalus* sp.
Cattle	Babesiasis or Red water	*Babesia bigemina*, *B. bovis*	*Boophilus* sp. *Ixodes* sp.
Horses	Babesiasis or Biliary fever	*B. caballi*, *B. equi*	*Rhipicephalus* sp.
Dogs	Babesiasis or Biliary fever	*B. canis*	*Haemaphysalis leachi*
Cattle Sheep	Heartwater	*Rickettsia ruminantium*	*Rhipicephalus* sp. *Ambylomma* sp.

All these diseases exist in tropical Africa but some of them, notably Anaplasmosis and Redwater, may occur in subtropical or even temperate zones. Except for *Babesia* infections there is no satisfactory cure for these tick-borne diseases, and control depends on eradicating or reducing the numbers of the intermediate host, the tick.

TICK CONTROL

The numerous genera and species belonging to the family Ixodidae are all tough-skinned parasites and are difficult to control because they spend part of their life cycle on the host and part on the ground or in crevices in the walls of the houses in which the animals live. They differ considerably in their habits, and the length of time spent on the host may vary greatly from species to species: some ticks may have alternate hosts such as small rodents and the like. These are points of great importance in planning control measures and a careful study of the life cycle of the more important ticks in any territory is required before adequate control measures can be instituted. The main method of tick control has been, and still is, by treating the host with an acaricidal fluid, either by dipping or spraying or applying the acaricide to the main sites of attachment on the body in the form of a grease or ointment. The period between dipping will depend on the life cycle of the tick. For instance, a three-host tick such as *Rhipicephalus* will require treatment at not less than weekly intervals because it lives only a few days on the host. On the other hand, when controlling the one-host tick of the genus *Boophilus* longer dipping intervals are possible since this tick spends a much longer time on the host.

In many cases control, as opposed to eradication, is to be preferred because in diseases such as Babesiasis and Anaplasmosis a degree of immunization or pre-immunization is acquired from a sublethal infection. It will be readily appreciated that when tick infestation is adequately controlled the general condition of the animals is greatly improved apart altogether from the absence of specific diseases.

ACARICIDAL SUBSTANCES USED IN TICK CONTROL

Arsenic, usually in some form of sodium arsenite, has held pride of place as a dipping fluid since the discovery by Smith & Kilbourne that the cattle tick was responsible for the transmission of Texas fever or Redwater some fifty years ago. Many tick-borne diseases have been eradicated by the efficient use of arsenic dips in the control of ticks but the modern insecticides of a much less poisonous character will inevitably replace arsenic as a means of control. BHC and DDT have now been used for some years with great success and they have been expecially useful in areas such as South Africa where the tick was becoming resistant to arsenic.

Resistance to these newer insecticides is however developing, especially in ticks of the genus *Boophilus*. More recently toxaphene has proved a most promising substance for tick control. It was thought that toxaphene had a useful residual protective action but is seems that a week is the longest interval that it is safe to leave an animal between treatments. This substance has proved very efficient for the control of species of *Ambylomma*, which transmits the disease known as Heart-water, a rickettsial infection of sheep, goats, and cattle. In addition to those named above there are many other diseases caused by ticks, and their control is essential if the development of a sound livestock industry is to be achieved.

THE TSETSE FLIES

This group of dipterous flies belonging to the genus *Glossina* comprises some twenty-seven species which with one exception are found only in tropical Africa. They transmit trypanosomiasis to man (Sleeping sickness) and animals (Nagana). Most species of *Glossina* and domestic stock are incompatible, and vast areas of Africa are devoid of cattle and man because of the tsetse fly. Before discussing control measures it is necessary to mention briefly the life history and some ecological data concerning *Glossina*. The tsetse is unique in that it is larviperous and gives birth to only one mature larva at a time, which is very different from many of the dipterous flies and ticks which lay large numbers of eggs giving rise to many larvae either on the ground or on the host. Control measures concerning *Glossina* are however mainly aimed at the adult fly and the methods adopted depend on the ecological background of the species involved. All tsetse require shade; some, such as the riverine species, e.g. *G. palpalis*, require heavy forest whereas others, such as *G. swynnertoni*, exist in very light dry scrub country. *G. pallidipes*, on the other hand, likes thickets, whilst *G. morsitans* favours the savannah bush of the well known Miombo type.

It should be remembered that tsetse flies themselves are relatively harmless and an uninfected fly is a nuisance but not a menace. The source of infection with the trypanosome is the game whose blood is the natural food of the fly, and this applies more particularly to the savannah or bush flies which are the most important from the disease aspect in animals. With a knowledge of the fly and the disease it transmits control of *Glossina* and trypanosomiasis resolves itself into the following headings.

(1) *Attacking the pupae*

Experimental biological control has been attempted in the laboratory but from the practical aspect this can be dismissed as a method of control.

(2) *The adult fly*

(*a*) *Bush clearing*. A knowledge of the breeding habits of certain species of *Glossina*, especially the savannah flies, has resulted in a method of selective clearing which has had considerable local success especially in Tanganyika, whilst local forest clearing along the lake shore or river banks is useful in the case of *G. palpalis* and *G. tachinoides*.

(*b*) *Late burning*. This method, which was introduced by Swynnerton, if well organized reduces the number of flies but has proved disappointing as a method of permanent control.

(*c*) *Trapping and hand catching*. Useful in very small localized areas but of no practical importance except as a means of assessing the fly population of an area.

(*d*) *Insecticides*. The newer insecticides have opened up a promising method of attack on the tsetse fly. Early laboratory experiments showed that *Glossina* is highly susceptible to DDT and BHC. Other insecticides such as chlordane and dieldrin are also lethal but most of the field work has been confined to the former chemicals. If the adult fly is going to be assailed by contact insecticides it will be appreciated that the type of cover is a most important factor and generally speaking the lighter the bush the more likely is the insecticide to come in contact with the fly, other factors being equal. The method of application will of course also have to be varied in accordance with the type of canopy to be penetrated, whether the insecticide is applied by aircraft or by other means. Following the pioneer field work in Zululand by the South African Government on the deposition of the insecticide by aircraft much work has been carried out in East Africa under the auspices of the Colonial Insecticides Committee.

The campaign in Zululand has so far been very successful and the tsetse there, mainly *G. austeni*, *G. pallidipes* and *G. brevipalpis*, have been virtually wiped out as indicated by bait cattle surveys. After much experimentation and practical experience the method now used is to deposit the insecticide in the form of an aerosol. This method of control raised a host of fundamental problems concerning the bionomics of the tsetse, methods of application, methods of assessing results, chemical, physical, and meterological problems and so on. These are being tackled and there is no doubt that the campaign against the tsetse, using insecticides, will become more efficient as time goes on, and it seems that deposition using aircraft will be the accepted method.

(*e*) *Defoliants.* A great deal of work has been done in this connexion by Prof. Blackman's team at Oxford, and promising trials have taken place in Africa using aircraft to deposit the defoliants. Thus an attack with defoliants followed by an insecticide is possible and is probably the method of tsetse control of the future.

(3) *The trypanosome*

Theoretically, if an efficient prophylactic against the trypanosome can be used in the mammalian host the tsetse fly as a disease transmitter is much reduced in importance. Much work has been done on chemoprophylaxis, and some drugs will protect animals for appreciable periods in the presence of tsetse, but there are formidable practical difficulties to be overcome before this can become an established long-term control measure. Nevertheless, it is proving very useful in certain cases, e.g. during movement of cattle through tsetse belts to markets or to fresh grazing grounds.

(4) *Game*

By destroying the game and therefore the food supply of the fly. In some parts of Southern Rhodesia success against *G. morsitans* has been claimed by this method. In the early part of this century tsetse disappeared from the Northern Transvaal following an epizootic of Rinderpest which killed much of the big game, and there is no doubt that certain species of *Glossina* are very sensitive to variations in the game population, especially some of the larger species such as buffalo.

In spite of all these methods of control the tsetse fly still remains as one of the great problems in the development of Tropical Africa, and it is only by constant endeavour and research that the solution will be found so that the great areas of land now empty except for the wild game will be made available to man and his farm stock.

Taylor, T. H. C. (1955). *Ann. appl. Biol.* 42, 190–196

BIOLOGICAL CONTROL OF INSECT PESTS

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The term 'biological control' has been generally used during the last 50 years to mean the control of an insect or plant pest by means of one or more parasitic or predatory insects introduced deliberately, but it would be more appropriately used in a much wider sense to cover all biological methods of control, as opposed to chemical and physical methods.

One of the main objects of these Jubilee meetings is to survey the achievements of the last half-century in each of the selected branches of applied biology and outline present trends and probable future developments. It seems to me that the most profitable course to pursue in the short time available to me is to consider first whether the successes in this field during the period under review are such that biological control, in the narrower sense of the term, can be regarded as a method that is comparable in general value to chemical methods, in particular; and then to consider whether biological methods in the widest sense should be developed for use in the future, in conjunction with chemical measures or as alternatives to them. It is quite usual, in generalizing on the control of pests, to speak or write as though there are two main alternative methods available, the biological and the chemical; as though, in fact, these two are on a par in general usefulness. This occasion seems a good one to consider whether this is true.

I do not propose to describe in detail the successful cases of control by introduced natural enemies. In the first half of the period under review, there were several notable instances, and for the present purpose it is sufficient to remind you of the control of Coccids on citrus in California and elsewhere by Coccinellids, the control of a Delphacid and a weevil on sugar-cane in Hawaii, the former mainly by a Mirid and the latter by a Tachinid, and the control of three pests of coconut palms in Fiji, a Zygaenid moth, a Coccid and a Hispid beetle, by a Tachinid, a Coccinellid and a Chalcid. In these cases, complete biological control was attained and it has stood the test of time; the results were so dramatically satisfactory that they caused entomologists and others of that period to regard the introduction of natural enemies as the simplest and the most promising method of controlling insect pests in all parts of the world.

Since that time there have been a few other similarly successful cases. In the Seychelles, Coccids on coconut palms have been controlled by Coccinellids, and the Eucalyptus weevil in South Africa and Mauritius, the European wheat-stem sawfly in Canada, the white butterfly and the diamond-backed moth on cruciferous crops in parts of Australia and New Zealand, and the coffee Tortricid in Ceylon, have all been controlled by Hymenopterous parasites. It must be stressed, however, that the number of successes has been only a small proportion of the number of attempts made, and instances of complete, rapid and permanent results such as those obtained in Fiji and Hawaii many years ago must now be recognized as rare occurrences. Moreover, experience of the last 30 or 40 years inevitably suggests that most of the pest-control problems of that period that have been capable of entirely satisfactory solution by this method have already been solved by it, so that similar successes will be increasingly rare events in the future. Occasionally, insects will be introduced accidentally and become established in countries where they did not previously occur and in conditions such that they can thrive and become serious pests; but experience indicates that whereas in some of these cases complete control by natural enemies may be achieved, in most of them it will not.

It is often difficult to obtain from published accounts of the results of introductions of natural enemies a definite impression as to whether or not the desired degree of control has been obtained and maintained. The literature of this subject contains many statements to the effect that particular parasites have been introduced and successfully established, as though the establishment of natural enemies were in itself a satisfactory result. References to comparatively high percentages of parasitization, without corresponding statements about the effect on the pest populations, are also common, but knowledge of percentage parasitization without reference to the actual numbers involved is of little or no meaning in relation to control, since, in particular cases, even 99% destruction of a pest population is not enough to reduce the damage done by the pest to the desired level. Sometimes, no definite pronouncement is made as to whether the result attained is such as to make other measures unnecessary, and we are merely informed that a useful degree of control has been achieved. Such statements cause the reader to conclude that the results may have been inadequate or merely temporary. In general, the supporters of biological control in the narrow sense of the term have unwittingly given the impression in recent years that they are on the defensive against the supporters of chemical control and are reluctant to admit the limitations of their method. This impression may or may not be true, but its existence suggests that an attempt at an unbiased assessment of the value of the method is worth while.

The instances of biological control that I have so far mentioned are those in which the control has been so complete that nothing further is needed. There have been less than twenty cases in this category in our period of 50 years. There is a second category of cases in which the suppression of the pest has not been so thorough or extreme, but has nevertheless been so great in parts of the affected area that from the practical and economic point of view the results can fairly be claimed to be quite adequate in those parts. The case of the coffee mealy-bug in Kenya is probably in this category, as is that of the wood wasp in New Zealand and that of the woolly aphis in various countries. The next category is one in which the method begins to break down in competition with chemical methods; it comprises the numerous instances in which introduced enemies achieve some reduction in numbers of the pest, but not enough to render other measures unnecessary. In most of these cases, chemical measures which have been in use before the introduction of parasites or predators must be continued afterwards, so that nothing has been gained by the introductions. It is sometimes claimed in these circumstances that the parasites or predators introduced are useful because they supplement other control measures, but such a contention is unconvincing because modern insecticides, if used at all, are usually completely effective by themselves so that any supplementary method is superfluous. Farmers and other producers anxious to prevent or avoid damage by insects are the first to welcome biological control when it gives the results they desire because it costs them nothing, whereas chemical control involves a considerable outlay annually, but they will use insecticides, despite the annual cost, until other methods can be shown to result in higher incomes.

We are thus faced with a curious situation. We have in biological control a method of controlling pests which, at its best, is completely and permanently successful at no cost whatever except initially, and even the initial cost is relatively small and is usually borne by a government or a community. Yet, in general, it fails to compete with chemical methods, even though these involve annual expense, because it only succeeds in special circumstances which rarely occur. Unfortunately, these circumstances are still inadequately understood, so that the limitations of the method cannot be clearly defined. There are, however, certain features of its past history which are revealing and important in this connexion. Consideration of the successful cases leads to the conclusions that the method is more likely to succeed in islands than in continents, and in the tropics than in temperate countries; and conversely, that it is most unlikely to give satisfactory results in countries like Britain and other European countries, except in very special cases like that of white-fly in greenhouses.

Supporters of biological control have often argued and still argue that there is no reason why it should not be as useful in continental conditions as in island conditions. One would like to be able to support this view, but the evidence is too strongly against it. The oustanding successes have been in islands and good results obtained elsewhere have in the main been in areas which are comparable to islands in some respects, notably in that they are isolated by natural barriers and are limited and specialized in flora and fauna, as are parts of Australia, California and Kenya. The principal reason suggested for the greater success of introduced natural enemies in island conditions is that the relatively small fauna contains few or no species likely to attack any beneficial insect that may be introduced. The greater degree of success obtained in the conditions of tropical islands than in those of temperate countries is almost certainly due at least partly to the equable climate of such islands, which enables the introduced insects to breed continuously throughout the year and therefore to multiply very rapidly. Seasonal conditions unfavourable to breeding, such as winters in temperate countries and long periods of hot, dry weather in the continental tropics, seem to increase the hazards to which introduced species, not yet adapted to the climate, are exposed.

While it is possible to suggest these reasons for the special suitability of tropical islands for biological control, they are somewhat theoretical and are not sufficiently precise. In most attempts at biological control, parasitic or predatory insects, themselves little known ecologically, are introduced into conditions which are also inadequately known. There are only a few cases in which efforts have been made, by studying the pest in the country and in the conditions in which the control is required, to obtain in advance an idea of the sort of parasite or predator that might be expected to achieve satisfactory results, but in most cases the selection of natural enemies to be introduced has been made largely without fundamental investigation. The need for basic studies is probably greatest when the insect to be controlled has become a pest in the country in which it is indigenous, through a modification of its environment or the advent of some factor which renders the indigenous natural enemies that have previously kept it in check unable to do so any longer. In these circumstances, the parasites from which a choice is to be made must be obtained from a foreign host species other than that which is to be controlled and most parasite species could not succeed where several indigenous parasites have failed. Examples of indigenous insects which became pests in their own country and have been completely controlled are the coconut Hispid beetle and the coconut Zygaenid moth, both in Fiji; the former was controlled by a Chalcid which was selected on the basis of considerable knowledge, and the coconut moth (which, incidentally, was thought at the time to have been accidentally introduced into Fiji from an unknown overseas source but is now believed to be indigenous) was controlled by a Tachinid, the selection of which involved a considerable element of good fortune.

The control in tropical islands of introduced pests is less dependent as a rule on thorough fundamental studies, the requirements which the natural enemy that is to be introduced must fulfil being less rigid, and the choice therefore wider. However, even in tropical islands, special circumstances sometimes exist which make the control of particular introduced pests by this method difficult or impossible. A recent example is the case of the Coccids that have threatened to destroy the Bermuda Cedar in Bermuda. Thorough investigation of this problem has led to the conclusion that the tree is so susceptible to the Coccids that even a very low population of them, such as would normally be regarded as negligible, is very harmful, and the natural enemies introduced cannot suppress the Coccids to the still lower level required. A similar difficulty arises in the control of insects that are harmful as virus vectors, the degree of suppression needed in such cases being as a rule so great as to be beyond the capabilities of natural enemies; an example is afforded by the mealy-bug vectors of swollen-shoot disease of cacao in West Africa.

In the least complicated environments, such as those of tropical islands, careful study of a problem sometimes leads to successful control of the pest by means of a parasite that would probably not otherwise have been selected, but it must be admitted that it is never possible to predict with certainty the result of any particular introduction. In continental areas, the factors concerned in the establishing and multiplication of insects are so numerous and complex that prediction of results is useless and any attempt at the utilization of natural enemies can be little more than a process of trial and error. Numerous attempts to put biological control work of this kind on a mathematical basis have been made from time to time, but except in the simplest and most straightforward instances they have failed. In this connexion, it is worth noting that the late G. C. Ullyett, who made a special study of insect populations in relation to biological control by natural enemies, stated in a recently published paper* entitled 'Biomathematics and Insect Population Problems' that mathematics 'has not provided us with a more exact method of expressing our major problems and that its use in biology is, in general, extremely limited'. He went on to say that 'Present developments in mathematics are not adequate to deal with the complex situations found in Nature....' These statements are perhaps a little too severe when removed from their context, but in the main they are true when applied to natural enemies, and they serve to emphasize the difficulties with which attempts to make biological control more precise are faced.

I can best summarize my views on this sort of biological control by saying that I know it to be the best of all methods of controlling pests when it works, but that it seldom works and that there is little future for it in continental areas. I think that the present tendency to organize the moving of parasites and predators about the world on an ever-increasing scale, despite decreasing results, is unsound and is, therefore, to be regretted. The limitations of the method are inherent in it and will not be changed by organization. Moreover, attempts to use it in combination with chemical methods are, in general, foredoomed to failure, biological and chemical methods being incompatible. At the same time, being, I suspect, one of the few people in this country who have witnessed the spectacularly rapid, thorough and permanent control that can result from the introduction of natural enemies, with little initial cost and no subsequent cost, I am a strong supporter of it, and if my criticism of the present trends seems destructive, it is only because I am anxious to give a true picture of the situation as I see it.

If we admit, as I think we must, that biological control, in the present narrow sense of the term, is not going to solve many of our problems, then we must consider whether any other methods that can be termed biological are likely to be used to better advantage. This brings us into the field of ecological control, or control based on thorough knowledge of the ecology and population dynamics of the insects to be controlled. Here we are faced with the inescapable difficulty that an understanding of the ecology of any one species can be gained only by prolonged and intensive quantitative studies over a long period of years, and this is hardly practicable for all the species of insects that we wish to suppress. Nevertheless, there can be no doubt that the ecological approach is the right one and that chemical methods should, in general, be regarded as stop-gaps which give control during the time needed for ecological research. If the major problems in applied entomology can be shown to be solvable by ecological means, then some at least of the others will be similarly solved in due course. The striking results obtained in recent years with viruses for the control of the Alfalfa Butterfly and the Japanese Beetle in the United States are an encouraging example of what can be achieved by patient, fundamental research over a long period.

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* *Mem. ent. Soc. S. Afr.* no. 2, 1953.

Most of you will have read the recent excellent paper by Solomon* entitled 'Insect Population Balance and Chemical Control of Pests'. He concludes that entomologists should do all they can 'to foster the development of research and control measures which have an adequate ecological basis'. There is no need for me to repeat his arguments here. My object is to emphasize that the days of empirical biological control are past and that a new approach, based on fundamental biological studies of the insects themselves and the factors that cause their numbers to fluctuate, is essential. Natural enemies constitute just one of the many ecological factors that affect insect numbers and they are not necessarily the most important; in those cases in which the natural enemies are not known to be important in the normal ecology, it is hardly reasonable to move them about the world for control purposes.

There is already a widespread awareness of the need for more basic studies of insect populations in relation to the control of harmful species, and this has arisen not only from the discoveries that strains of insects resistant to insecticides can arise and that chemicals applied for the control of one pest can cause outbreaks of others, but also from a general feeling of uneasiness about the ultimate, accumulated consequences of the general application to the soil and to plants of highly toxic insecticidal chemicals. We are at present passing through a period of confusion and conflicting interests in which most of us are eager to be able to advocate ecological rather than chemical measures, but in the present state of knowledge the supporters of ecological measures often have none that they can advocate with sufficient conviction. This is an inevitable interim condition which only research and time can end. Some of the most formidable of the world's problems in applied entomology, such as those of locusts and tsetse flies, are at present being tackled by a combination of chemical and ecological measures which is to be regarded as only a means to a more satisfactory end. The outbreaks of mites and Coccids that have resulted from the general use of modern insecticides on fruit trees have had the advantage that they have caused intensive studies to be made in Canada, the United States and Britain of the whole complex of animal species inhabiting the trees, and while growers will continue to use insecticides and acaricides so long as they obtain a bigger financial return by doing so, ecological information which will probably be of great value ultimately is being obtained meanwhile. How such information will eventually be used we cannot yet judge, but the difficulties that have already arisen from the use of modern insecticides suggest that the time may come when it is generally felt that it is better in the long run to use ecological methods to maintain all the species in a particular association at a reasonably low population level than to use chemical methods to reduce the most harmful species to a much lower level. General acceptance of the advantages of such a policy cannot come until the fundamental knowledge needed to support it is available. Our aim should be to ensure that the ecological conditions that we create are such that potentially harmful animal species are not unduly favoured and that we have the knowledge necessary for modification of the environment of insects wherever this is desirable for their control in the interests of our health or economy. When this happy state of affairs is reached, insecticidal chemicals will probably still be needed occasionally, but they will be used, not as part of a seasonal routine, but as a means of reducing particular populations that might arise in exceptional circumstances.

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* *Chemistry & Industry*, 1953, pp. 1143–7.

Meanwhile, we in Britain can derive consolation from the thought that so long as we maintain our present agricultural and horticultural practice of growing a great variety of crops in a mosaic of fields and small plots separated by hedgerows and uncultivated areas, our entomological problems will rarely be severe in comparison with those of tropical countries and vast continental areas. We already have a system which gives us a relatively high degree of ecological control of insects, even though we do not yet fully understand how it works. In the still developing regions of Africa and Asia, on the other hand, development will almost certainly continue to create environments in which grave new entomological problems will arise, and it is in these continents particularly that control of insect populations by methods based on thorough knowledge of their biology and ecology is likely to be most needed.

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THE NATURAL HISTORY OF SHEEP BLOWFLIES IN BRITAIN

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(With 3 Text-figures)

From its earliest days the Association of Applied Biologists has had within its ranks, workers who have studied various aspects of the sheep blowfly problem. The names of Wardle, Maldwyn Davies, Hobson and MacLeod come to mind, and the following account, rests largely on the foundations laid by these investigators.

1. BLOWFLIES WHICH ATTACK SHEEP

MacLeod's survey (1943*a*, *b*), based on an analysis of over 1000 samples of larvae collected from strikes occurring in various parts of the British Isles, demonstrated quite clearly that *Lucilia sericata* (Mg.) was the principal species responsible for sheep myiasis. Totalling the results obtained in his own survey and those of MacDougall (1909), Davies (1934) and Haddow & Thomson (1937), MacLeod showed that the percentage occurrence of the different species was: *L. sericata* (Mg.) 96%, *L. caesar* (L.) and *L. illustris* (Mg.) 10%, *Protophormia terrae-novae* (R–D.) 3%, *Calliphora erythrocephala* (Mg.) 2%; *C. vomitoria* (L.) less than 1%. The incidence of species other than *Lucilia sericata* was greatest in the north-west and least in the south-east of Britain. Thus, north and west of a line from Inverness to Glasgow only 53% of the samples contained pure cultures of *L. sericata*, whereas in central and east England the number had risen to 99%.

2. BREEDING SITES OF SHEEP BLOWFLIES

It follows from MacLeod's survey that sheep suffering from myiasis will in most cases carry a high percentage of *L. sericata*. Furthermore, as Maldwyn Davies (1934) showed, larvae while on the sheep are free from the attacks of parasites such as *Alysia manducator* and many of them, by the time a shepherd recognizes a 'struck' sheep are capable of completing development without further feeding. Samples of wool clipped from struck sheep in the course of dressing the animals have yielded over 1000 *Lucilia sericata* from individual sheep (Cragg, unpublished observations).

The *Lucilia* and *Calliphora* species have long been recognized as flies associated with carcasses, and in the period 1942–6 the present writer investigated the yield of blowflies obtained from different types of carrion. The work carried out at Aber, Caernarvonshire, was largely confined to carcasses exposed under conditions suitable for *Lucilia sericata* activity. Carcasses produced in late autumn to early spring when *Lucilia* spp. were not available were successfully colonized by *Calliphora* spp. and/or *Protophormia*.

For our present purpose, the principal results obtained in these studies can be demonstrated by reference to two sets of carcasses.

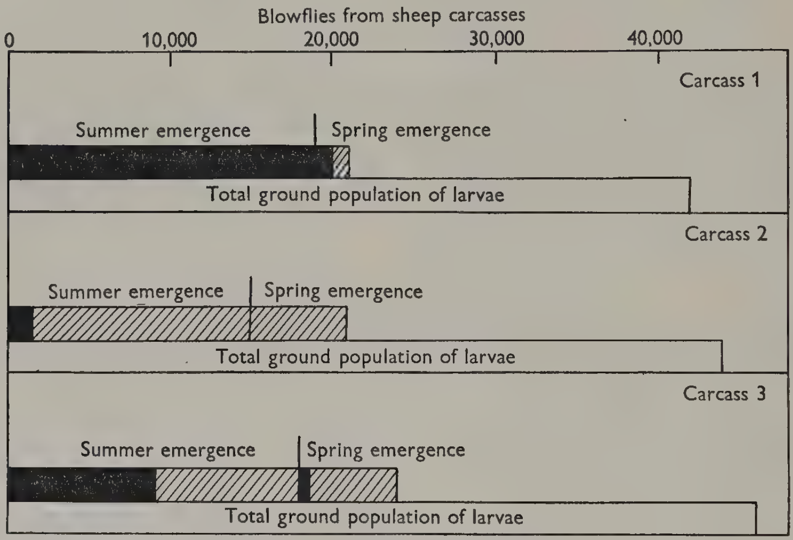

Fig. 1. Black represents *L. sericata* emergence and hatching *L. caesar* emergence. The carcasses were exposed to blowfly attack in June–July under conditions particularly favourable for *L. sericata* activity.

Sheep carcasses

Fig. 1 shows the numbers of blowflies obtained from the carcasses of three sheep killed at the same time and exposed to blowfly attack simply by laying them on the ground and allowing flies to oviposit on them. Carcass 1 was heavily infested with *Lucilia sericata* larvae before death, carcass 3 slightly infested and carcass 2 was without infestation.

From these and some twenty other sheep carcasses studied the following observations are worth noting:

Only carcasses infested with *L. sericata* at the time of death gave a preponderance of this species. In some carcasses where myiasis did not occur before death, the species, within the limits of the sampling techniques used, appeared to be absent from the fauna, and when present it rarely formed more than 10% of the emerging population.

Where *Lucilia* species colonized a carcass under open conditions, *Calliphora* species, although common visitors, rarely formed more than 2% of the emerging population. Larvae of these species would be present on carcasses in the later stages of decomposition but they suffered considerable mortality through the action of predators. They were the principal species which emerged from carcasses occurring in late autumn and winter.

Protophormia was an important member of the fauna particularly in the early part of the blowfly season when it would successfully compete with either the *Calliphora* or *Lucilia* species and form a major part of the emerging population.

The two types of carcass, those of sheep infested before death (the *myiasis* carcass) and those of sheep free from such infestation (the *non-myiasis* carcass) show marked differences in the physical characteristics of decomposition. In the *myiasis* type, larval activity results in the maintenance of high temperatures (40° C. +) throughout the 5–8 days following death when abundant food is available for the larvae. Thus eggs already present at the time of death, and in the main these have been laid by *L. sericata*, hatch rapidly and the larvae are full-fed before competitors become established in any number. On the *non-myiasis* carcass, the body temperature falls and post-mortem changes occur before larvae appear. Hatching and growth take place slowly and 2–4 days elapse before any marked rise in temperature is recorded. Temperatures as high as those in the *myiasis* carcass are typically confined to small areas where larval activity is intense. Waterhouse (1947) considered that high temperatures on sheep carcasses might be responsible for some 50% of the mortality of those larvae which escaped predation and parasitism. There was no evidence, in the British investigations that high temperatures were responsible for any marked degree of mortality.

Mention should be made of the habit of some blowfly species to move considerable distances from their feeding site once they have become full-fed. Herms (1907), for instance, pointed out that distances exceeding 20 ft. might be traversed. The survival value of this reaction has often been ignored in investigations on the fauna of carcasses but it plays a large part in limiting the period of time for concentrated activity by predaceous Diptera and Hymenopterous parasites. Fig. 2 shows the distribution of the principal Dipterous predators, *Ophyra leucostoma* and *Hydrotoea* spp. (mainly *dentipes*) and *Lucilia* species around a carcass. These populations were estimated from soil samples and field emergencies recorded under traps set at different distances from the carcass which was also enclosed in a trap just prior to the beginning of fly emergence. It is evident that the predaceous species do not move far from the carcass. Of the blowflies not recorded in Fig. 2, *Protophormia terrae-novae* when it occurred pupated on the carcass, attaching itself firmly by an adhesive secretion. *Calliphora* spp. were distributed in a manner similar to the *Lucilia* spp.

The burial of carcasses, although necessary for sanitary reasons, can raise the yield of *L. sericata* from negligible proportions to the level expected from a *myiasis* carcass. This results from the fact that *L. sericata* is often the first colonizer and if

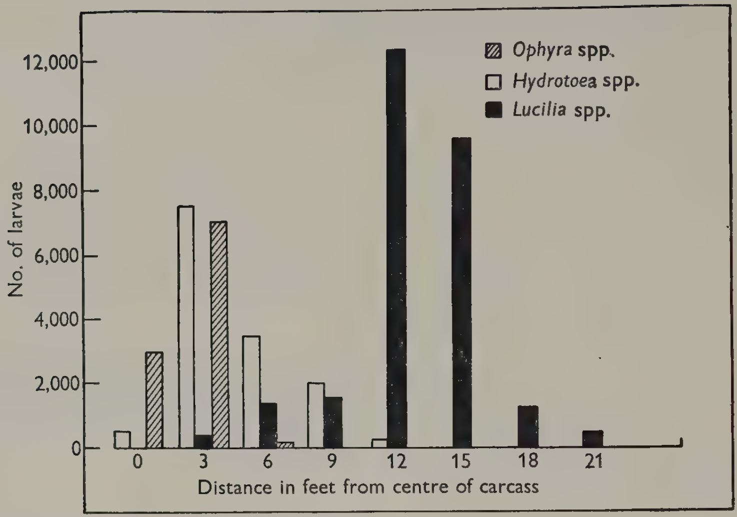

Fig. 2. Distribution in the soil around a sheep carcass of full-fed larvae of the principal dipterous colonizers.

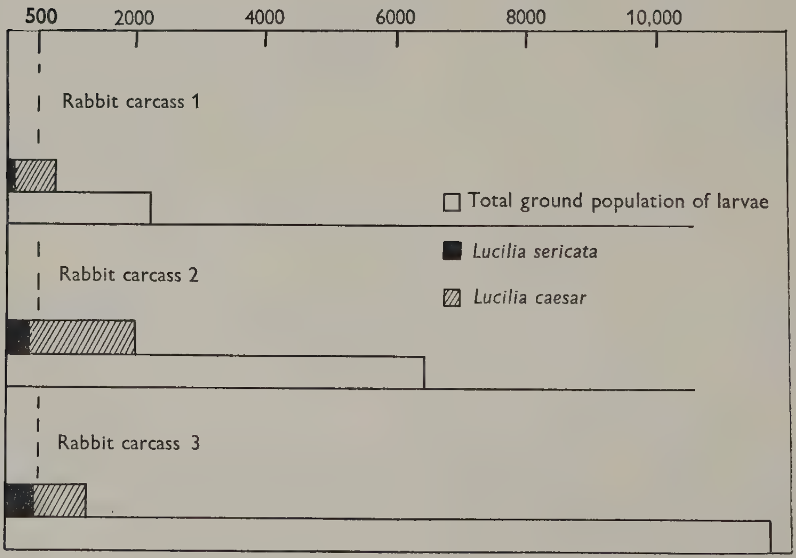

Fig. 3. Fly emergence from the larval populations produced from rabbit carcasses. The carcasses were exposed to blowfly attack in July under conditions particularly favourable for *L. sericata* activity.

burial takes place within 3–4 days of death the predominantly *L. sericata* population present as eggs or larvae, is given considerable protection from competition, predators and parasites.

Small carcasses

In proportion to their bulk, small carcasses could give a higher yield of *L. sericata* than was obtained from the *non-myiasis* type of sheep carcass. Yields from rabbit carcasses studied by the same methods as used for sheep carcasses are shown in Fig. 3.

That *L. sericata* forms such a small part of the total yield of blowflies from carcasses appears all the more surprising when the following facts are taken into account. Under open conditions it is more efficient at finding fresh carcasses than are the other species and it oviposits more readily on such carcasses. Further as L. Davies has shown (personal communication) the development period of its eggs is markedly shorter than that of other species with the exception of *L. illustris* which equals it and its eggs are capable of developing under drier conditions than are those of *L. caesar*, *L. illustris*, the two *Calliphora* species and *Protophormia terrae-novae*. Thus, the advantages conferred on the species by its efficient olfactory reactions and its more rapid egg development are outweighed by its failure to withstand the effects of inter-specific competition in the feeding phase.

It would be unwise to conclude from these studies that under farm conditions, the heavily infested sheep or the carcass of such an animal is the major source of *Lucilia sericata*. It may have been true on badly shepherded hills before the advent of modern insecticides but it is doubtful whether it applies to any part of Great Britain to-day. Perhaps it should be pointed out that Waterhouse (1947), writing in the days before DDT, concluded that in Australia the living sheep was by far the most important breeding ground for *L. cuprina*.

The contribution of naturally occurring small carcasses is difficult to assess, in the absence of adequate information on the quantities that may occur. The results quoted above, both for sheep and small carcasses were obtained under conditions highly favourable for *L. sericata* activity, and yet this species formed a small proportion of the populations which emerged. Under shaded conditions such as occur in thick hedgerows and woodland, the species is usually completely absent from the emerging fauna. On the other hand, scattered portions of a 'blown' carcass broken up by birds or mammals may present *L. sericata* with conditions almost as favourable as the buried carcass. Quantitative information on the relative population densities of *Lucilia* spp. does not exist. On the basis of trapping studies and field observations in rural habitats in Cumberland, Durham, Westmorland and North Wales, the present writer is of the opinion that *L. caesar* and *L. illustris* typically outnumber *L. sericata*, although in certain habitats *L. sericata* will be dominant. Thus, the field observations on the differences in density of the *Lucilia* species agrees to some extent with their relative densities in the fauna which emerges from *non-myiasis* sheep carcasses and rabbit carcasses.

It is evident from Green (1951) that other breeding media may be available even for *L. sericata.* He recorded large numbers breeding in pig food which as far as could be ascertained consisted only of vegetable matter. Further, he found the species ovipositing on fresh tripe-dung and (personal communication) he has recorded it as a common inhabitant of domestic refuse. At one refuse disposal centre in London he found high populations of larvae falling from railway trucks containing refuse. Whether dung forms an important breeding medium under rural conditions is doubtful. Although Thomsen & Hammer (1936) found it breeding in pig-dung in Denmark neither Hammer (1941) in Denmark nor Laurence (1953) in England found *Lucilia* species in naturally occurring cow-dung.

3. MOVEMENTS OF BLOWFLIES

Cragg & Hobart (1955) have shown by hand-marking over 3000 field-caught *L. caesar* in August–September 1943 that the major part of the population did not show extensive movement. On the assumption of a maximum radius of movement of 5 ml. some 60% of the marked flies remained within half a mile of the point where they were liberated. These observations were made on flies which had already reached the oviposition stage. It is possible that in the pre-oviposition condition, blowflies may move over large distances. Some preliminary studies on hand-marked, laboratory-bred *L. sericata* supported such a conclusion. In these marking experiments there was also some evidence that the area where *L. caesar* was marked was a region of special preference for the species, and therefore it is possible that the dispersal rate was lower than would have been recorded in less suitable areas.

A point of some biological importance which emerged from the marking experiments was that a life of 6 weeks was not unusual for female *L. caesar* in the latter part of the blowfly season.

The actual population estimates obtained are of little value but the number of flies trapped are of interest in view of the work of Gilmour, Waterhouse & McIntyre (1946) in Australia. They estimated the population of *Lucilia cuprina* to be 0·3–5·7 per acre. In the British experiments, on the days when attempts were made to estimate population densities the average catches were *L. sericata* 0·6 per acre and *L. caesar* 3·0 per acre. These figures indicate very large differences in the fly densities studied in the two investigations.

4. SUSCEPTIBILITY, ATTRACTION AND OVIPOSITION

Hobson (1935, 1936) made the most important contribution to our knowledge of susceptibility when he showed first, that larval excreta placed on living sheep was a specific attractant for gravid females of *L. sericata* inducing them to oviposit and secondly, that the same responses occurred when ammoniacal-rich substances were used. He advanced the hypothesis that two things were necessary for susceptibility: a live-sheep factor (S) and a putrefactive factor (P). Later, Cragg & Ramage (1945) demonstrated that the living sheep was not necessary, some oviposition being possible when the Hobson-type attractant was exposed in the middle of a clipped fleece. They also showed the importance of sulphydryls in bringing about attraction but not oviposition. On the basis of these observations they proposed as a working hypothesis, that fleece keratin under the action of sunlight and bacteria might be the source of attractive substances such as ammonia, carbon dioxide, hydrogen sulphide and organic sulphydryls.

Cragg (1950*a*) and Cragg & Thurston (1950) extended these studies, but showed that the results of exposing known attractants on sheep and using the attractants alone, gave different results. On sheep, *L. sericata* was the only species which appeared to oviposit in response to the presence of various chemicals, whereas the same materials, particularly a mixture of hydrogen sulphide and ethyl mercaptan, when used in traps mainly caught *L. caesar* and *L. illustris*. Again, oviposition was of relatively rare occurrence when the substances were used in traps.

Some of the differences just described have now been resolved (Cragg, 1955) by using an apparatus which reproduced some of the conditions associated with attractants when exposed on sheep. Using this 'artificial sheep' the importance of temperature in producing the full oviposition response has been clearly demonstrated. It has, for example, been possible to produce an amount of oviposition comparable with that occurring on the living sheep by exposing at 38–39° C. substances known to provoke oviposition on sheep.

Furthermore, by watching the behaviour of flies settling on the surface of the apparatus instead of trapping them, an explanation can be offered for the apparent differences observed in earlier studies. It is evident that sulphur-rich mixtures are general attractants to which *L. caesar*, *L. illustris* and to a smaller extent, *L. sericata* will respond. If, in addition, ammonium carbonate is present, *L. sericata* will invariably oviposit, whereas the other species rarely do so. Thus the apparently contradictory results obtained when using the same materials on sheep and in traps can now be reconciled. On sheep, whilst *L. caesar* and *L. illustris* might alight on the animals, they would not normally oviposit and would not, under the system in use, be recorded as 'attracted to' sheep. In traps, all visitors would be recorded and therefore the *L. caesar* group would invariably outnumber *L. sericata*.

Using the artificial sheep it was soon evident that an important part of the attraction mechanism, was the presence of sheep wool. In the absence of this covering the amount of settling and oviposition was much reduced. It was clear that sheep wool provided some stimulus which could not be entirely replaced by sulphydryl compounds.

Laboratory experiments (Cragg & Cole, 1955) using a choice-chamber technique have shown that some olfactory stimulus is intimately associated with sheep wool to which female *L. sericata* are particularly sensitive. Furthermore, they have demonstrated differences in behaviour between different blowfly species and different strains of *L. sericata*. Flies from various sources in Britain, ranging from 'Town Bred' to 'Sheep Bred' flies have given the same degree of response. On the other hand, British *L. sericata* differ significantly from Australian and Danish strains. Apart from establishing that some wool factor existed to which *L. sericata* reacted, these studies, and those of Cragg (1950*b*) made in Denmark where myiasis is of very rare occurrence, support the view that no clear-cut distinction can be drawn between supposed sheep and carrion strains of *L. sericata*.

Although in the above descriptions of behaviour the reactions have been described rather as though the blowfly were a puppet and that it was only necessary to pull the right string in order to obtain a response, such descriptions are an over-simplification of the animals' reactions. There exists a whole series of stages in behaviour towards olfactory stimuli varying from the initial exploratory activities to the fulfilment of the oviposition act. In the three *Lucilia* species referred to above, once an individual has explored the main stimulus it may continue to explore the area where the stimulus was exposed, even after the complete removal of the stimulus. Further, there is an element of mutual or social stimulation which may be very pronounced. Thus, a group of flies attracted to a stimulus, may themselves act as an attractant (Cragg & Ramage, 1945). The same effect can result in oviposition taking place more readily. Finally, Cragg & Thurston (1950) have shown that there are changes in behaviour with season and altitude.

5. MICROCLIMATE AND THE ESTABLISHMENT OF MYIASIS

It has long been recognized that moisture is important for the production of myiasis. Davies & Hobson (1935) concluded that a humidity of over 90% R.H. was necessary for at least 14 hr. from the occurrence of oviposition to ensure egg development, hatching and the establishment of first-instar larvae.

That eggs laid naturally on sheep run the risk of death by desiccation was demonstrated by MacLeod (1937) who recorded that out of sixty-four egg masses found on a flock, only twenty-nine gave rise to myiasis in spite of other conditions being favourable. It is clear from Davies (1948*a*, *b*) that the earlier figure of 90% R.H. for 14 hr. is an overestimate. Thus at 37° C. and 60% R.H. he recorded 40–90% hatching in spite of the fact that at 37° C., the minimum humidity for development is approx. 50% R.H. In recent years too much attention has been given to humidity requirements at 37° C., the conclusion of W. M. Davies (1934) that 31° C. was the average temperature at the site of egg deposition having been overlooked. The present writer has confirmed and extended W. M. Davies's work. He has shown that eggs are rarely laid at sites where temperatures exceed 34° C., the majority of batches being laid 2–4 cm. from the skin surface where the range was 28–34° C. While the minimum humidity necessary for hatching does not vary markedly over the range 25–38° C. the capacity of the eggs to develop is greatly affected. L. Davies (1948*a*) has shown that at 30° C. and 25% R.H., a humidity well below the level normally recorded on sheep, some 68% of the eggs successfully completed development. Furthermore, at that temperature, larvae could withstand imprisonment in the egg for periods exceeding 5 hr. (L. Davies, personal communication). A suddden rise in humidity to 60–80% R.H. would allow a high percentage of the eggs to hatch. Davies & Hobson (1935) stated that 'first-instar larvae do not produce a wound (which will supply food and moisture) in less than 5 hr.'. Thus the high humidity of 90% R.H. necessary for the survival of larvae at skin temperature need not be maintained for more than 5 hr. Whether, in fact such a high humidity is essential for the whole of this period is open to question. The investigations on fleece microclimate already quoted and others (MacLeod, 1939; Cragg, 1950*b*) indicate that at the skin surface, humidities higher than 80% R.H. occur infrequently and are associated with high rainfall or special circumstances such as very warm weather which induce sweating. The risks of desiccation to the first instar will be reduced if a large number of egg batches are concentrated on one small area. The mutual stimulation effect that comes into play when large numbers of blowflies are attracted to a sheep often ensures the formation of a consolidated mass of eggs. Within such masses the microclimate favours successful development of the centrally placed eggs and many larvae which emerge may reach the second instar by feeding on dead or dying individuals. Once the larvae have established themselves on the skin and are producing excreta then, provided that suitable weather conditions occur, the success of the strike is ensured.

6. GENERAL CONSIDERATIONS

While some features of the behaviour and ecology of blowflies are now much better known than they were some 10 years ago, much remains to be done before we can say that we understand the problem of sheep myiasis.

We are still ignorant of the changes occurring on sheep which make them attractive to blowflies. The views often expressed that susceptibility is dependent upon bacterial action or a combination of bacterial action and sunlight are no more than working hypotheses. Admittedly the bacterial origin of susceptibility receives some direct support from Australia where it is known (see Mackerras & Mackerras, 1944 for literature) that the condition 'fleece-rot' which renders sheep attractive, is bacterial in origin. So far (Cragg, 1955) it has not been possible in Britain, to bring about attraction simply by incubating moist wool at 38° C., under field conditions. Bacteria likely to be involved in the production of attractive substances may of course be associated with the skin rather than the wool fibre or they may be dependent for their activity on skin secretions. There is little doubt that the bacterial flora of the skin and fleece should receive more attention than it has been given in the past.

In the fields of behaviour and ecology, studies on species other than *L. sericata* should be extended. It has already been pointed out that behaviour may be modified by climate. So far, studies using the 'artificial sheep' have been confined to an area where *L. sericata* is the only species known to cause myiasis. It would be worth while repeating these studies in an area where one of the other species is of major importance.

Perhaps of paramount importance for the completion of an account of blowfly natural history is the need for some investigations on the behaviour and ecological requirements of male blowflies. Under field conditions they are difficult to find and do not necessarily react to the same attractants as females.

Much of this review has been concerned with investigations started in the pre-DDT days, when sheep myiasis was a disease of major importance in Great Britain. With the advent of DDT and BHC, suitable materials for preventing myiasis were available. Recently, Stones *et al.* (1954) have demonstrated the great efficiency of Dieldrin. The problem now is not so much what to use, but how to apply it. In spite of the success which has been achieved it is important to remember that the actual conditions producing the disease are not yet understood. It is unlikely that the present high cost of prevention both in materials and labour, will be reduced until more information is available on the origins of susceptibility. The need for studies on the bacteriology and physiology of the skin and fleece of the sheep is obvious. At the same time, the general biological nature of the problem must not be forgotten. It is in response to changes on the sheep that the blowfly lays its eggs. This oviposition response can be brought about under a variety of conditions and there still remains the task of providing a comprehensive explanation of the features leading to oviposition whether it be on a living animal, a carcass or in a dust-bin.

REFERENCES

CRAGG, J. B. (1950*a*). The reactions of *Lucilia sericata* (Mg.) to various substances placed on sheep. *Parasitology*, **40**, 179–86.

CRAGG, J. B. (1950*b*). Studies on *Lucilia* species (Diptera) under Danish conditions. *Ann. appl. Biol.* **37**, 65–79.

CRAGG, J. B. (1955). In preparation.

CRAGG, J. B. & COLE, P. (1955). In preparation.

CRAGG, J. B. & HOBART, J. (1955). In preparation.

CRAGG, J. B. & RAMAGE, C. R. (1945). Chemotropic studies on the blow-flies *Lucilia sericata* (Mg.) and *Lucilia caesar* (L.) *Parasitology*, **36**, 168–75.

CRAGG, J. B. & THURSTON, B. A. (1950). The reactions of blowflies to organic sulphur compounds and other materials used in traps. *Parasitology*, **40**, 187–94.

DAVIES, L. (1948*a*). Laboratory studies on the egg of the blowfly *Lucilia sericata* (Mg.). *J. exp. Biol.* 71–85.

DAVIES, L. (1948*b*). Observations on the development of *Lucilia sericata* (Mg.) eggs in sheep fleeces. *J. exp. Biol.* **25**, 86–102.

DAVIES, W. M. (1934). The sheep blowfly problem in North Wales. *Ann. appl. Biol.* **21**, 267–82.

Davies, W. M. & Hobson, R. P. (1935). The relationship of humidity to blowfly attack. *Ann. appl. Biol.* **22**, 279–93.

Gilmour, D., Waterhouse, D. F. & McIntyre, C. A. (1946). An account of experiments undertaken to determine the natural population density of the sheep blowfly, *Lucilia cuprina.* Weid. *Bull. Coun. sci. industr. Res. Aust.* no. 195, pp. 39.

Green, A. A. (1951). The control of blowflies infesting slaughter houses. I. Field observations on the habits of blowflies. *Ann. appl. Biol.* **38**, 475–94.

Haddow, A. J. & Thomson, R. C. M. (1937). Sheep myiasis in South-west Scotland, with special reference to the species involved. *Parasitology*, **29**, 96–116.

Hammer, O. (1941). Biological and ecological investigations on flies associated with pasturing cattle and their excrement. *Vidensk. Medd. dansk. naturh. Foren. Kbh.* **105** (pp. 257).

Herms, W. B. (1907). An ecological and experimental study of Sarcophagidae with relation to lake beach debris. *J. exp. Zool.* **4**, 45–83.

Hobson, R. P. (1935). Sheep blow-fly investigations. II. Substances which induce *Lucilia sericata* (Mg.) to oviposit on sheep. *Ann. appl. Biol.* **22**, 294–300.

Hobson, R. P. (1936). Sheep blow-fly investigations. III. Observations on the chemotropism of *Lucilia sericata* (Mg.). *Ann. appl. Biol.* **23**, 846–51.

Laurence, B. R. (1953). Some Diptera bred from cow dung. *Ent. mon. Mag.* **89**, 281–3.

MacDougall, R. S. (1909). Sheep maggot and related flies. *Trans. Highl. agric. Soc. Scot.* **21**, 135–74.

Mackerras, I. M. & Mackerras, M. J. (1944). The attractiveness of sheep for *Lucilia cuprina. Bull. Coun. Sci. industr. Res. Aust.* no. **181**, pp. 144.

MacLeod, J. (1937). The nature, epidemiology and control of sheep myiasis in Britain. *J. comp. Path.* **50**, 10–32.

MacLeod, J. (1939). The moisture balance of the living sheep in relation to blowfly myiasis. *Ann. appl. Biol.* **27**, 379–92.

MacLeod, J. (1943*a*). A survey of British sheep blowflies. *Bull. ent. Res.* **34**, 65–88.

MacLeod, J. (1943*b*). A survey of British sheep blowflies, II. *Bull. ent. Res.* **34**, 95–111.

Stones, L. C., Wood, J. C. & Hart, C. B. (1954). The use of Dieldrin for sheep maggot control. *Vet. Rec.* **66**, 183–7.

Thomsen, M. & Hammer, O. (1936). The breeding medium of some common flies. *Bull. ent. Res.* **27**, 559–87.

Waterhouse, D. F. (1947). The relative importance of live Sheep and of Carrion as breeding grounds for the Australian Sheep Blowfly *Lucilia cuprina. Bull. Coun. sci. industr. Res. Aust.* no. 217, pp. 31.

Soil-borne pests and diseases

Garrett, S. D. (1955). *Ann. appl. Biol.* 42, 211–219

A CENTURY OF ROOT-DISEASE INVESTIGATION

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My credentials for attempting this brief historical survey are simply stated. During my first 3 years' research work on the take-all disease of cereals, the results of which are neither published nor publishable, I managed to make most of the mistakes made by most of the pioneers of root-disease investigation. This has enabled me to view the achievements of these early workers with insight, and no less with admiration.

In what follows, I shall distinguish three phases in the history of root-disease investigation, under the headings of etiology, environment and microbial ecology. In its first two phases, root-disease investigation has followed the general pattern of development in mycological plant pathology, from which it can in no way be distinguished. In its third phase, in which we are living to-day, root-disease investigation has come to be recognized as belonging no less to soil microbiology than to plant pathology. Such distinctions between different phases of development in any science, and especially their attempted delimitation in time, can at best be only a serviceable approximation to truth, having some validity as regards the behaviour of a majority of individual investigators. Every generation has its own great men, who are much ahead of their time, though they do not always succeed in hastening materially the general speed of advance in their science.

First phase—etiology

In the first three-quarters of the past century, root-disease investigation was simply a branch of plant pathology, and a somewhat neglected branch at that. Root-disease investigation could advance no faster than the rest of plant pathology; in actual fact, it advanced more slowly, for a variety of reasons. In air-borne diseases of plant shoots caused by fungi, the first of Koch's (1882) four postulates,* constant association of the suspected parasite with the disease, is frequently obvious to the most casual observer, through sporulation of the fungus on the diseased host plant. In most soil-borne diseases, on the other hand, the fungal parasite is not macroscopically obvious on the roots, on which it seldom sporulates *in situ*, and fungal fructifications on the stem above ground are not infrequently those of secondary parasites and saprophytes. For this reason, fungal parasites were not usually the most likely amongst possible causes of root disease to the early investigators. Supposing, however, that one of these pioneers of root-disease investigation, by dint of careful observation, had established the likelihood of a parasite as causal agent on the basis of Koch's first postulate, the courage of his convictions alone was not always adequate to the task of complying with the requirements of the other three postulates. Inoculation experiments failed more often than not; the most frequent cause of failure was inadequacy of the artificial inoculum. It is only of recent years that we have come to understand the reason for such failures; for successful infection, the *inoculum potential* of the parasite must be sufficient to overcome the resistance to infection of the host plant. It thus happened that although Texas root rot of cotton was correctly attributed to a species of *Ozonium* (now renamed *Phymatotrichum omnivorum*) by Pammel in 1890, the first successful experimental inoculations were not performed until some 33 years later, by King (1923) and by Taubenhaus & Killough (1923).

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* Koch's four postulates for establishing the cause of a parasitic disease are (1) constant association of the organism with the disease, (2) isolation of the organism in pure culture, (3) reproduction of the disease by inoculation with the pure culture of the organism, (4) re-isolation of the organism, and identification with the original inoculant.

At other times, this difficulty over inadequate inoculum potential in inoculation experiments was too successfully surmounted. By the use of too high a dosage of inoculum, especially in association with environmental conditions (such as that of freshly sterilized soil) unusually conductive to infection, it was possible to produce an artificial syndrome or even a new disease. With such experimental artifacts from the glasshouse to complicate a problem already sufficiently difficult, it was not surprising that earlier investigators sometimes incriminated a harmless fungus, or were left to scratch their heads over the difficulty of reproducing field symptoms of a disease in pot experiments.

SECOND PHASE—THE ENVIRONMENT

Throughout the nineteenth and well into the twentieth century, root-disease investigators were mainly occupied with determination of the causes of various important but still obscure root diseases. During those years, the parasitic origin of disease was still a sufficiently new idea to make this first and most essential step in investigation almost an end in itself, beyond which it must have seemed premature to look and certainly pessimistic to doubt further progress. Eventually, however, important diseases of undetermined causation became notably scarcer, and this phase of root-disease investigation drew gradually to its close.

The difficulties of direct control of soil-borne diseases by means of fungicides must always have been obvious enough; during the second decade of the present century, more workers began to consider possibilities for indirect control, through appropriate manipulation of the cultural environment of the growing crop. Thus was initiated, by L. R. Jones and his associates at Wisconsin, an extensive programme of investigation into the effect of environment upon soil-borne diseases. A monographic account of this work has been published by Jones, Johnson &

Dickson (1926). An outstanding figure in the history of plant pathology, L. R. Jones can well be acclaimed as the founder of modern root-disease investigation. Envisaging with rare insight the direction that further effort should take, Jones provided the means whereby to reach this end. The famous Wisconsin soil-temperature tanks were designed for the study of soil-temperature effects upon plant disease, and these tanks were the progenitors of controlled environment chambers and glasshouses. Soil temperature and moisture content were the factors chiefly studied by Jones and his associates in their work upon soil-borne disease. By concentrating upon these two factors in particular, it was possible to collate results from the temperature tank studies with field records of disease incidence, in regions of the U.S.A. with widely different temperature and rainfall characteristics. This conjunction of thorough field study with glasshouse experimentation has taken all that was best from the nineteenth century into the twentieth century.

THIRD PHASE—MICROBIAL ECOLOGY

The modern era of root-disease investigation may be said to have commenced a quarter of a century ago. Up to this time, root-disease investigation had not differed in any essential respect from any other branch of mycological plant pathology, the origins of which have been recently reviewed by Brown (1951). It was perhaps the established orthodoxy of the plant pathologist's approach to the problem of an unknown disease that temporarily held up further advances. The very experimental method that had made possible such spectacular discoveries in the elucidation of etiology was now to delay further progress, because used with insufficient discrimination. In the experimental analysis of any situation, it is permissible and even essential to construct an artificial model that will enable the effect of a single factor to be isolated and studied. The use of such an experimental analogy will become dangerous only if the model becomes mistaken for the reality outside its appropriate sphere of usefulness. This artificial model for root-disease experimentation was created by the first workers who used sterilized or partially sterilized soil for inoculation experiments, in attempting to determine the cause of some particular disease under investigation. The factor to be studied in isolation was the suspected pathogen. It was therefore necessary to eliminate other possible root parasites from the soil to be used for such inoculation experiments. Only those inoculation experiments conducted with this precaution carried conviction; honesty also proved to be the best policy, and scientific rectitude was rewarded by the best conditions for the success of such inoculation experiments that could possibly have been devized, though this good fortune was not appreciated at that time. This artificial model of the root environment worked admirably for so long as its use was limited to its original purpose, that of investigation into the etiology of yet obscure diseases. The use of this model became dangerous, however, when continued into the second phase of root-disease investigation, that of environmental studies upon disease behaviour. Although, by this time, as much was known about general soil microbiology as about diseases of plants, it is a curious fact that, for yet a further period, the great majority of root-disease investigators virtually ignored the existence of the soil's microbial population. Plant pathologists were trained and assigned to the study of soil-borne diseases, and soil microbiologists to the study of biological problems of soil fertility; an administrative convenience seemed to have become an intellectual barrier.

Eventually it was recognized that the general microbial population of the soil, a factor in the root environment hitherto almost wholly ignored by plant pathologists, was indeed the most important factor of all, so far as root-disease fungi were concerned. As we all know, many important discoveries have been anticipated by voices crying in the wilderness; in the fullness of time, other and more effective voices have at last made themselves heard. In this instance, the effective voices that aroused root-disease investigators to realization that they were studying the host-parasite relationship in at least a partial microbiological vacuum seem to have been those of Sanford (1926) and of Millard & Taylor (1927). Following up Millard's (1921) work on control of potato scab (*Streptomyces scabies*)* by green manuring with grass cuttings, Sanford suggested that such control might be due to the antagonistic effects of saprophytic bacteria developing upon the decomposing green manure. Millard & Taylor (1927) independently announced, shortly afterwards, that the development of scab on potatoes grown in sterilized soil inoculated with *S. scabies* could be much reduced by simultaneous inoculation of the soil with *S. praecox*, an obligate saprophyte of more vigorous growth habit. Sanford & Broadfoot (1931) then provided further evidence for this general hypothesis by showing that infection of wheat seedlings by *Ophiobolus graminis* could be completely suppressed, under appropriate conditions, by the antagonistic action of various individually co-inoculated species of fungi or bacteria.

General recognition of these new opportunities for plant pathologist and soil microbiologist alike was hastened by Fawcett's (1931) most timely Presidential Address to the American Phytopathological Society on the need for experimentation with deliberately mixed as well as with pure cultures of micro-organisms. From personal experience, I can vouch for the electrifying effect of these and other communications upon those of us who were struggling with our own particular root-disease problems at that time. Nor can I forbear to mention the first of a brilliant series of papers by Weindling (1932) upon the parasitism of the plant pathogen, *Rhizoctonia solani*, by the common soil fungus *Trichoderma viride*, which culminated in isolation of the antibiotics gliotoxin (Weindling & Emerson, 1936) and viridin (Brian & McGowan, 1945). An even brighter light was shed upon our immediate problems, perhaps, by Henry's (1932) masterly experimental analysis of an interaction between temperature and antibiotic effects in a study of the take-all disease of cereals (*Ophiobolus graminis*).

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* Terminology of Waksman (1950).

The marriage between plant pathology and soil microbiology, now consummated, was followed by a honeymoon period of unbounded optimism, during which the most extravagant hopes were entertained for the progeny of the union, to be christened 'Biological Control'. The first optimistic forecasts of the prospective god-parents, amongst whom I was one, were dimmed by anxiety when it was eventually realized that the pregnancy would be unexpectedly long and difficult. One child, indeed, was still-born, and was quietly laid to rest under a tombstone inscribed 'Biological Control by Inoculation of the Soil with Antagonistic Micro-organisms', though some of the bereaved claim that it was buried alive and is, in fact, still faintly breathing. Other children of the marriage, though at first puny, are yet alive and slowly progressing, and more promising ones will assuredly be born in due course.

From the beginning, it had been possible to predict the failure of attempts at biological control of soil-borne diseases by inoculation of the soil with 'antagonistic', i.e. antibiotic-producing, micro-organisms. Long before this, ecologists studying vegetation had shown that successful establishment of any plant species could occur only in a habitat favouring its success in competition with other species, as had been foretold by Darwin in *The Origin of Species*. It is always possible that an exotic micro-organism having the required characteristics for exerting biological control may also be able to establish itself as a normal inhabitant of cultivated soils, but this is unlikely. As Stanier (1953) has pointed out, the distribution of non-parasitic soil micro-organisms is cosmopolitan; most micro-organisms occur in most soils, because most soils comprise an endless variety of micro-habitats, 'hundreds or even thousands of which lie concealed from the gross ecological eye in any gram of soil'. Truly exotic micro-organisms are therefore hard to find; as it happens, however, most attempts at biological control of root diseases through soil inoculation have been made with micro-organisms reintroduced, in much larger numbers, into the type of soil from which they had been isolated in the first place. Such attempts to boost numbers of a selected antagonistic micro-organism by heavy inoculation of the soil can exert only a transient effect upon the population of that organism in the soil; a higher population level can be permanently established only by making the appropriate change in the soil habitat. The truth of this contention was demonstrated by Weindling & Fawcett (1936), in a model experimental analysis of the biological control by *Trichoderma viride* of the damping-off disease of citrus seedlings due to *Rhizoctonia solani*.

It is no longer possible to doubt that the normal microflora of the soil does exert a natural biological control of most, if not all, soil-borne diseases of plants. This is demonstrated by the more rapid and intense development of most soil-borne diseases when the pathogen re-invades soil that has been either completely or even partially sterilized by heat or by fumigants. In completely sterilized soil, a pathogen may actually kill a species of higher plant that is normally immune to it, as demonstrated by Eaton & Rigler (1946) for *Phymatotrichum omnivorum*; the Texas cotton-root rot fungus does not attack monocotyledons in the field, but maize seedlings were killed by it when grown in completely sterilized soil inoculated with the fungus.

The problem therefore confronting us is to find methods of increasing the degree of biological control normally exerted by the soil microflora. In soils that have been sterilized or partially sterilized for eradication of root-disease fungi, it is essential to hasten natural recolonization of the soil by its normal microflora, as was first pointed out by Hartley (1921). If conditions in the treated soil are such as to favour recolonization by a microflora more effective in biological control, this will be better still. This new and exciting possibility has become apparent since it was first observed that the fungus flora developing in soils treated with certain fumigants was quite different in proportional composition from that of the soil before treatment. The new fungus flora is frequently dominated by *Trichoderma viride*, some strains of which produce significant quantities of either gliotoxin or viridin (Brian, 1951). The prolonged dominance of *T. viride* in formalin-treated soil was demonstrated by Warcup (1951, 1952), who ascribed it to the exceptional tolerance of this fungus to formalin. *T. viride* is markedly tolerant of several other chemicals used as soil fumigants; its dominance as a recolonizer of treated soil may be ascribed either to differential survival, or to the fact that it is able to recolonize treated soil in the wake of the dispersing fumigant, at concentrations of the chemical that are still fungistatic for its competitors. After a prolonged experimental study of soil fumigation with carbon disulphide for control of *Armillaria mellea* in Californian citrus orchards, Bliss (1951) has provided substantial evidence for his hypothesis that eradication of *A. mellea* is not due to an immediately fungicidal effect of the fumigant, but must be attributed, at least in part, to the much augmented population of *Trichoderma viride* developing in the fumigated soil.

The effect of organic manures, and especially of fresh organic material, in sometimes assisting control of such diseases as take-all of cereals, Texas root rot of cotton, and potato scab, has been attributed to the activity of saprophytes decomposing the organic material. Such control must remain empirical, and therefore unreliable and inextensible, until its mechanism has been elucidated. I myself have attempted to analyse this effect of organic manures in controlling the take-all disease (Garrett, 1936–48), following the first report of successful control by Fellows (1929). In any such epidemiological analysis, it is necessary to consider possible effects of soil treatment upon (1) parasitic activity of the fungus upon the roots of the growing crop, (2) survival of the fungus in the absence of its host, (3) resistance of the host plant to development of the disease. I have shown that in so far as decomposing organic material contributes to soil respiration, it must increase the concentration of carbon dioxide at the root surface, and hence is likely to depress speed of growth and infection by *Ophiobolus graminis*. Fresh organic material poor in available nitrogen decreases longevity of *O. graminis* in infected crop residues; organic material high in available nitrogen has the opposite effect. During the growing period of the cereal crop, a high nitrogen content of the soil increases the rooting capacity of the crop (unless other nutrients are limiting), and hence enables it to tolerate a considerable degree of root infection without appreciable loss of yield. This last effect of organic manures yielding available nitrogen in decomposition was first demonstrated by Clark and his associates (Clark, 1942; Stumbo, Gainey & Clark, 1942), following upon earlier findings of a similar effect exerted by inorganic nitrogenous (and phosphatic) fertilizers. It is thus evident that organic manures of different composition can exert opposite effects upon a single disease, and also that opposite effects can be produced even by the same manure acting upon different components of the host-parasite equilibrium.

The control of Texas root rot of cotton by organic manures, first demonstrated by King, Hope & Eaton (1934) and attributed by them to increased microbiological activity, has been further analysed by Mitchell, Hooton & Clark (1941), who found that organic material stimulated spontaneous germination of the sclerotia of *Phymatotrichum omnivorum*, in the absence of living host roots. Consequent dissipation of the sclerotia as vegetative mycelium led to a considerable decline in the population of these resting bodies. Such an effect cannot be described as 'biological control' in the usual sense of this term.

It is now known that control of potato scab by green manuring is not always successful; KenKnight (1941), for instance, reported substantial *increases* in scab after green manuring. The conditions under which green manuring exerts control of the disease are not yet understood, nor is the frequent occurrence of severe scab on the first crop of potatoes taken after ploughing-up old grassland (Moore, 1943). The need for further study of *Streptomyces scabies* in its actual soil environment is thus all too apparent.

The main conclusion to be drawn from these investigations into biological control of soil-borne diseases is that such attempts will be successful only if integrated with the most thorough and exhaustive general studies of root-disease epidemiology. Towards this end, we have developed a number of precise laboratory techniques whereby the behaviour of root-disease fungi can be examined in a controlled soil environment. Such experimentation in the laboratory and glasshouse is an essential complement to continued study of root-disease behaviour in the field. The knowledge thus obtained can be used to further root-disease control through various permutations of crop rotation, cultivation, manuring and soil amendment, as well as by the production of disease-resistant varieties of crop plants. Set against our avowed objective of integrating root-disease control with good crop husbandry, the advocacy of expensive special control measures, however ingenious and spectacular, must be a confession of failure. Success in this task will win at least the appreciation of the discerning few, such as are gathered together at this Jubilee Conference of the Association of Applied Biologists. A forgotten disease is the pathologist's most worthy memorial.

REFERENCES

BLISS, D. E. (1951). The destruction of *Armillaria mellea* in citrus soils. *Phytopathology*, **41**, 665.

BRIAN, P. W. (1951). Antibiotics produced by fungi. *Bot. Rev.* **17**, 357.

BRIAN, P. W. & MCGOWAN, J. C. (1945). Viridin: a highly fungistatic substance produced by *Trichoderma viride*. *Nature, Lond.*, **156**, 144.

BROWN, W. (1951). Mycology over a century. *Advanc. Sci., Lond.*, **8**, 214.

CLARK, F. E. (1942). Experiments towards the control of the take-all disease of wheat and the *Phymatotrichum* root rot of cotton. *Tech. Bull. U.S. Dep. Agric.* no. 835.

EATON, F. M. & RIGLER, N. E. (1946). Influence of carbohydrate levels and root surface microfloras on *Phymatotrichum* root rot in cotton and maize plants. *J. agric. Res.* **72**, 137.

FAWCETT, H. S. (1931). The importance of investigations on the effects of known mixtures of organisms. *Phytopathology*, **21**, 545.

FELLOWS, H. (1929). Studies of certain soil phases of the wheat take-all problem. *Phytopathology*, **19**, 103.

GARRETT, S. D. (1936–48). Soil conditions and the take-all disease of wheat. I–X. *Ann. appl. Biol.* **23**, 667; **24**, 747; **25**, 742; **26**, 47; **27**, 199; **28**, 14, 325; **31**, 186; **35**, 14, 435.

HARTLEY, C. (1921). Damping-off in forest nurseries. *Dep. Bull. U.S. Dep. Agric.* no. 934.

HENRY, A. W. (1932). The influence of soil temperature and soil sterilization on the reaction of wheat seedlings to *Ophiobolus graminis*. *Canad. J. Res.* **7**, 198.

JONES, L. R., JOHNSON, J. & DICKSON, J. G. (1926). Wisconsin studies upon the relation of soil temperature to plant disease. *Res. Bull. Wis. agric. Exp. Sta.* no. 71.

KENKNIGHT, G. (1941). Studies on soil actinomycetes in relation to potato scab and its control. *Tech. Bull. Mich. agric. Exp. Sta.* no. 178.

KING, C. J. (1923). Cotton root rot in Arizona. *J. agric. Res.* **23**, 525.

KING, C. J., HOPE, C. & EATON, E. D. (1934). Some microbiological activities affected in manurial control of cotton root rot. *J. agric. Res.* **49**, 1093.

KOCH, R. (1882). *Über die Milzbrandimpfung, eine Entgegnung auf den von Pasteur in Genf gehaltenen Vortrag*. Berlin: Fischer.

MILLARD, W. A. (1921). *Rep. Univ. Leeds & Yorks. Coun. agric. Ed.* no. 118, 8.

MILLARD, W. A. & TAYLOR, C. B. (1927). Antagonism of micro-organisms as the controlling factor in the inhibition of scab by green manuring. *Ann. appl. Biol.* **14**, 202.

MITCHELL, R. B., HOOTON, D. R. & CLARK, F. E. (1941). Soil bacteriological studies on the control of *Phymatotrichum* root rot of cotton. *J. agric. Res.* **63**, 535.

MOORE, W. C. (1943). Diseases of crop plants; a ten years' review (1933–42). *Bull. Minist. Agric., Lond.*, no. 126.

PAMMEL, L. H. (1890). Cotton root rot. *Rep. Tex. agric. Exp. Sta. for* 1889, p. 61.

SANFORD, G. B. (1926). Some factors affecting the pathogenicity of *Actinomyces scabies*. *Phytopathology*, **16**, 525.

SANFORD, G. B. & BROADFOOT, W. C. (1931). Studies of the effects of other soil-inhabiting micro-organisms on the virulence of *Ophiobolus graminis*. *Sci. Agric.* **11**, 512.

STANIER, R. Y. (1953). Adaptation, evolutionary and physiological: or Darwinism among the micro-organisms. *Adaptation in Micro-organisms. Third Symp. Soc. gen. Microbiol.* Cambridge University Press.

STUMBO, C. R., GAINEY, P. L. & CLARK, F. E. (1942). Microbiological and nutritional factors in the take-all disease of wheat. *J. agric. Res.* **64**, 653.

TAUBENHAUS, J. J. & KILLOUGH, D. T. (1923). Texas root rot of cotton and methods of its control. *Bull. Tex. agric. Exp. Sta.* no. 307.

WAKSMAN, S. A. (1950). *The Actinomycetes*. Waltham, Mass.: Chronica Botanica.

WARCUP, J. H. (1951). Effect of partial sterilization by steam or formalin on the fungus flora of an old forest nursery soil. *Trans. Brit. mycol. Soc.* **34**, 519.

WARCUP, J. H. (1952). Effect of partial sterilization by steam or formalin on damping-off of sitka spruce. *Trans. Brit. mycol. Soc.* **35**, 248.

WEINDLING, R. (1932). *Trichoderma lignorum* as a parasite of other soil fungi. *Phytopathology*, **22**, 837.

WEINDLING, R. & EMERSON, O. H. (1936). The isolation of a toxic substance from the culture filtrate of *Trichoderma*. *Phytopathology*, **26**, 1068.

WEINDLING, R. & FAWCETT, H. S. (1936). Experiments in the control of *Rhizoctonia* damping-off of citrus seedlings. *Hilgardia*, **10**, 1.

Rishbeth, J. (1955). *Ann. appl. Biol.* 42, 220–227

ROOT DISEASES IN PLANTATIONS, WITH SPECIAL REFERENCE TO TROPICAL CROPS

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It is still true, as Garrett (1944) pointed out, that any discussion of root disease in plantations must chiefly be concerned with diseases of tropical crops. That more is known about root diseases of rubber and tea than about those of almost any plantation crop of temperate countries is doubtless mainly due to the greater value of the former crops. But anyone who has seen the crippling loss of timber through butt rot by *Fomes annosus* in a spruce plantation or the havoc wrought by *Armillaria mellea* in a fruit orchard may be pardoned for wondering why in the past these parasites have not been more fully studied in Great Britain, for instance. In the short survey which follows the aim will be to show how field observations and fundamental work on certain root-infecting fungi have indicated possible methods of control, and what degree of success has attended the application of such methods.

With tropical crops, the association between root disease and stumps of the original forest trees has long been recognized. After such trees have been felled, wood-rotting fungi such as *Fomes lignosus* occupy the stumps, often spreading far along the roots, where sooner or later they are in a position to infect the interlacing roots of crop plants. Although many tropical root parasites have well organized mycelial strands or rhizomorphs, which may grow short distances through soil, the great majority of infections occur where stump root and tree root are in actual contact. Sources of root disease are provided not only by stumps of original forest trees but by those of trees taken out during thinning of closely planted crops and by those of shade trees removed during growth of the plantation. An interesting example from Java of the relation between red root disease of tea, caused by *Ganoderma pseudoferreum*, and root systems of the susceptible shade tree, *Albizzia falcata*, is given by Schoorel (1949).

How do tree stumps become infected with these parasites? Of the many ways in which this might occur, the two most likely would seem to be invasion of the stump from portions of root infected before felling and infection of the cut surface by air-borne spores. Petch (1921) working in Ceylon, held that the latter was the more important method, and although no experimental evidence was produced to support this belief, protection against air-borne infection was sought by stump extraction or by cutting trees below soil level and covering the stump surface with soil. By contrast, Napper (1932–40), working in Malaya, became convinced by field observations that spore infection of stumps occurred rarely if at all, and that the sources of disease were infected roots of the original forest trees. Napper thought that in natural forest communities such trees are more or less in equilibrium with their root parasites, and that this balance is upset by felling, after which losses from root disease become more serious. An early experiment at the Rubber Research Institute in Malaya showed that the incidence of the root parasite *Fomes lignosus* on young trees 2½ years after planting was lower at sites where roots had been left *in situ* after felling the forest trees than at sites where most of the roots had been removed and was lower still where secondary forest had been allowed to grow up. Napper explained this by the behaviour of *F. lignosus* rhizomorphs in relation to their food-base and to the availability of root surfaces other than those of susceptible young rubber trees. A similar effect to that of secondary forest, in the presence of which root infections of the plantation trees were relatively scarce, was later obtained with cover crops by Cronshey & Barclay (1939).

Whether Napper's explanation of these effects is entirely correct may be open to doubt, but their reality is not: as a result of these discoveries a new and successful method for dealing with root diseases in young plantations was evolved. After the forest was felled, the ground was cleared of the larger stumps and the rubber trees planted. Thereafter trees were inspected 2 or 3 times a year for rhizomorphs of root-disease fungi: if any were found on the upper tap root or laterals, the root system was further excavated until the source of infection and the whole extent of the invading mycelium had been discovered. All infective material and those portions of young tree root already penetrated by the parasite were then removed, as were the epiphytic rhizomorphs, which in the case of *F. lignosus* extend some 5–15 ft. ahead of the infected part of the root. Napper found that with regular inspections of this kind it was possible to bring a young plantation through a heavy attack of root disease without losing more than 20% of affected trees. The efficiency of this method was largely dependent on the rhizomorph habit of *F. lignosus*, the dominant root parasite in plantations on cleared forest sites: if the rhizomorphs had been epiphytic for a much shorter distance in advance of penetration, as for instance with *Ganoderma pseudoferreum*, far more trees would have been lost.

Various complications arose when sites already bearing rubber were replanted: for instance, distinction could be made between patches where root disease was manifest in the previous stand and intervening areas where the earlier crop was apparently healthy. With the former, *G. pseudoferreum* caused considerable loss which, however, as Napper showed, could be reduced by removing infected roots before planting. With the latter, trouble was to be expected both from *Fomes noxius* and from *F. lignosus*. Most of the *F. noxius* infections were traceable to contact of the rubber trees with logs lying on the soil surface, which were thought to have become infected by wind-borne spores after felling. Napper could not explain satisfactorily how *F. lignosus* arose after replanting apparently healthy stands of rubber, but he was inclined to think it originated from old infections which had lain dormant until brought into activity by felling. A very similar situation was recorded by Murray (1938) in Ceylon, where *F. lignosus* or *Poria hypobrunnea* caused root infections on young rubber trees established on sites previously bearing healthy rubber.

It had for some time been suspected that the resistance of tree roots to latent or localized infections was sharply lowered by felling, and a clear demonstration that this was so with *Armillaria mellea* was provided by Leach (1937, 1939), working on tea in Nyasaland. Whereas very few trees were killed in virgin forest by this fungus, after felling the roots of several species became extensively invaded. On the other hand, relatively few of the species shown by experiment to be susceptible to *A. mellea* were associated with affected tea bushes in plantations. Leach suggested that many species escape infection because their roots die rapidly after felling, before the parasite reaches them from existing centres of infection; once the roots are dead and have been invaded by saprophytes it cannot enter them. By contrast, roots of other species such as *Parinarium mobola* die very slowly and *A. mellea* has a greater chance not only of reaching but of extensively colonizing them. Tea plantations established on the site of former pure stands of *Parinarium* were in fact often severely damaged. It was further discovered that for its growth *A. mellea* required roots with a high starch content and also that if *Parinarium* trees were ringed some time before felling their roots soon became depleted of starch, died quickly and became invaded by harmless saprophytes instead of *Armillaria mellea*. This last most interesting observation was turned to practical effect, and ring-barking of trees before felling has provided a simple and effective means of reducing losses from *A. mellea*. A good instance of this is recorded by Wiehe (1952), who found that the practice of ring-barking indigenous forest trees before planting tung (*Aleurites montana*) in Nyasaland has reduced the incidence of the pathogen: no less than 10 times the amount of oil is lost in non-treated areas than in treated ones. It would be interesting to know whether in temperate countries ring-barking could be employed to check growth of *Armillaria mellea*.

Some of Napper's later experiments suggest that similar effects can be obtained with other root parasites. Thus poisoning of rubber stumps with sodium arsenite caused the roots to die more quickly than usual and favoured their invasion by saprophytes rather than by *Fomes lignosus*. In plots where stumps had been treated in this way the incidence of root disease from this parasite was low. Napper too found that ring-barking or poisoning led to rapid depletion of starch in roots, this effect being most striking with a combination of frill-girdling and poisoning carried out before felling. Once again there was a fairly close relation between the rate of starch loss and that of invasion by saprophytic fungi. In practice, however, stump poisoning is still in an experimental stage, the chief drawbacks to its general adoption being the restricted penetration of the poison into the root system and the high cost of dealing with any remaining sources of infection, owing to the large bulk of roots left in the soil.

Turning now to root disease in conifer plantations, we find in the behaviour of *Fomes annosus* several interesting parallels with that of tropical root parasites.

F. annosus is widely distributed in the northern hemisphere, particularly severe disease outbreaks being recorded from Europe, where the parasite may either kill trees outright or cause heart rot in the lowest and most valuable portion of the stem. The disease received attention well before the end of the nineteenth century and important discoveries were made, notably by Hartig (1894), who stated for instance that the fungus spread from root to root where these were in contact or had fused. Here, as with several other diseases, the early investigator was correct; but 60 years later there is still disagreement on the mode of radial spread, some workers holding that the fungus grows from tree to tree through the humus layer. The presence of small *F. annosus* sporophores in the litter of some diseased plantations has very probably contributed to this belief, but such sporophores are invariably attached to small infected roots. Experimental evidence and field observations (Rishbeth, 1950–51) suggest strongly that the fungus characteristically inhabits stumps and roots and cannot grow freely in soil owing to competition from other organisms. This point is of practical as well as theoretical interest since several suggested methods for controlling the parasite are based on the assumption that it inhabits soil, and one even involves liming to discourage its growth through soil. This treatment actually has the opposite effect to that intended, since *F. annosus* spreads more freely from root to root in alkaline than in acid soils, the root surface microflora in the latter soils tending to be more antagonistic to it.

Once again the mechanism of stump infection is a matter of considerable importance. In East Anglian pine plantations (*Pinus silvestris* and *P. nigra var. calabrica*) it is noteworthy that trees on former arable or heath become infected with *F. annosus* only after certain operations such as cleaning, thinning or rack-cutting: initially they are free from root disease, by contrast with trees established on former woodland, which are often infected from stumps almost at the outset. Operations which allow *F. annosus* to enter healthy plantations have one thing in common: they produce stumps, either of young conifers, of small hardwood trees, such as *Betula pendula* or even of bushes, such as *Ulex europaeus*. There is convincing evidence that such stumps are infected by wind-borne spores of *Fomes annosus*, which are freely produced by sporopheres in this forest area. Spores alighting on the exposed wood germinate under suitable conditions and the mycelium grows down through the body of the stump into the lateral roots, along which it spreads at the rate of about 1 m. per year. Even in early stages of stump colonization other wood-inhabiting fungi compete with *F. annosus*; in general the latter only becomes established if it reaches the stump within a week or two of felling, before the wood has been invaded too extensively by other fungi. Within 1½–2 years of felling, *F. annosus* has grown sufficiently far along the stump roots to infect living roots of adjacent trees; thereafter the stump roots remain infective until *F. annosus* is replaced by other fungi. The rate of this replacement depends, for instance, on the size of stump and on the composition of the soil microflora: it may take only a year or two but sometimes, as with large stumps in some alkaline soils, it may still be incomplete 30 years after felling. With such a long potential survival in stumps it is clearly imperative to prevent or limit initial stump infection at least at sites where the disease is likely to be serious. The incidence of stump infection by *F. annosus* was found to be greatly reduced by painting or creosoting the stump surface immediately after felling: in one experiment only 4% of such stumps contained the parasite a year after felling, whereas 36% of comparable untreated stumps were infected by it (Rishbeth, 1952). Covering the stump surface with soil gave no protection against *F. annosus* in this experiment. In those East Anglian plantations considered liable to serious attacks, stump treatment with a suitable protectant is now a routine measure during thinning: it is perhaps too early to assess its effect but reports from foresters tend to be favourable.

Unfortunately this procedure cannot prevent *F. annosus* growing into stumps from roots already infected at the time of felling. In regularly thinned plantations, however, observations suggest that far fewer stumps are infected this way than by air-borne spores. In areas of more natural forest growth such as N. Sweden and much of N. America, where, incidentally, sporophores of *F. annosus* are much scarcer, the relative importance of the two modes of stump infection may well be reversed. It can in fact be argued that *F. annosus* causes extensive damage in Europe largely because it has much greater opportunities for colonizing stumps than in natural or semi-natural forest, an important additional factor being the establishment of many plantations on soils disturbed by agricultural usage. One obvious solution of the problem of infection, suggested from tropical experience, is stump extraction, but the difficulty and cost of this method probably render it impracticable. That it would be effective in eliminating early root infection of young conifers in the following rotation cannot be doubted from the results of a recent large-scale stump extraction experiment in Holland.

There is urgent need for further information about conditions influencing infection of stumps by air-borne spores and about other possible modes of stump infection. Serious attempts should be made to limit the growth of *F. annosus* already present in stump roots and, if possible, to replace this fungus by encouraging growth of vigorous competing saphrophytes such as *Peniophora gigantea*. And clearly, with other root parasites, it is necessary to re-assess the importance of wind-borne spores in initiating new centres of infection.

So far, particular stress has been laid upon the activities of the parasite, as opposed to the condition of the host, because the view is taken that an understanding of the mode of life and ecological status of the parasite is essential in formulating methods of control. If evidence were needed of the importance of host resistance in determining the course of root disease in plantations, it could readily be found in East Anglia, where pines show a marked increase in resistance to *Fomes annosus* at the age of about 25 years, chiefly as a result of increased resin production by the roots. Again, there is a marked tendency in the same area for conifers to be more resistant to *F. annosus* on acid soils than on alkaline ones, which may partly be due to the generally greater moisture-retaining capacity of the former soils. Observations from many parts of the world, supported by some experimental evidence, suggest that resistance of conifers to *F. annosus* is low where the soil is abnormally dry. Destruction of litter and humus by burning, in so far as it reduces water-retaining capacity of a soil, is thus probably detrimental, and in this connexion an interesting parallel exists between the behaviour of *F. annosus* on young pines and that of *F. lignosus* on young rubber: with each the incidence of root disease is markedly greater when the former forest sites are burned after clearing than when no burning takes place. Disturbance of the forest soil profile, which occurs to some extent with stump extraction and is carried to an extreme with arable cultivation, may likewise prove deleterious: here of course other important changes, such as in soil microflora, are involved. For combating root diseases in plantations we are greatly in need of further information about the fundamental requirements for healthy tree growth in terms for instance of soil structure and microbiology. On the other hand, there is plenty of scope for applying what is already known, for example in correct selection of the crop for particular sites, where possible, in restricting forest operations known to favour root disease, such as thinning, and in attempting to improve water relations in the soil.

No survey of plantation root diseases, however brief, would be complete without a reference to vascular wilts, since banana and cotton, to mention only two tropical crops, are affected by wilt diseases of major economic importance. Although for sake of brevity attention will here be confined to work on *Fusarium* wilt of bananas, largely carried out in the Caribbean area (Wardlaw, 1935), this disease has much in common with vascular wilts of other crops. One distinctive feature of vascular wilts, not as yet of particular importance with the other root diseases so far discussed, is the existence of resistant varieties: for instance the highly esteemed banana variety Gros Michel is susceptible whereas its recent successors in the West Indies, such as Lacatan, are resistant, although less satisfactory in some other respects.

Recent work in Jamaica (Rishbeth, 1955) confirms the earlier opinion of Hansford (1926) that the causal organism, *F. oxysporum* f. *cubense*, is indistinguishable morphologically from the widely distributed soil saprophyte *F. oxysporum* and can thus be differentiated only by a suitable host test. The pathogen occurs in a wide range of soil types, and its abundance is greatly affected by the presence of bananas. Despite its relative scarcity in soil, it has a marked competitive advantage over saprophytes since it can invade susceptible plants and grow extensively in them. After collapse of the plant and subsequent breakdown of its tissues, the pathogen returns to the soil in greatly increased numbers. Here, in the absence of its host, its numbers rapidly decline and after about 10 years it cannot be detected by any test; yet its continued survival is well established by many field observations on the incidence of wilt.

F. oxysporum f. *cubense* is dispersed in many ways, for instance by infected planting material, by contaminated tools and in soil and plant debris, especially by flood water. Thus in Jamaica, plantations on alluvium were in general free from wilt until serious flooding occurred, and it is noteworthy that banana cultivation in hill country was a major factor leading to soil erosion, consequent severe flooding in the river valleys and hence to spread of the disease. Soil erosion and a less obvious but significant decline in soil fertility undoubtedly played a major part in the earlier development of disease in this island. To-day there are just a few scattered plantations of Gros Michel still virtually free from wilt after 20 years or more of continuous cultivation. These have a number of features in common, for example, the soil is well aerated, medium to heavy in texture, alkaline in reaction and usually very rich in available potash. In other situations, where one or more of these features is lacking, Gros Michel shows its more usual susceptibility to wilt: hence a wide range of agricultural soils are now unable to support a commercial crop of this variety.

The two factors which above all render control of wilt in a susceptible variety so difficult are the lengthy survival of the pathogen in soil in the absence of bananas, and the tendency for plants to become infected when the soil population of the pathogen is extremely low. Passive measures of control such as trenching and destruction of infected plants were extensively used in the past but these, although restricting radial spread of wilt to some extent, did not prevent new scattered outbreaks elsewhere in a plantation. It might be thought that knowledge of the conditions associated with existing healthy plantations could be applied in devising methods of soil treatment, but unfortunately little or no success has attended experiments involving applications of organic or inorganic fertilizers. A greater knowledge of the conditions for uptake from the soil of important nutrients such as potash might promote further progress in this direction.

Methods of soil disinfection have in general proved disappointing, but reference must be made to 'flood-fallowing', which is employed by the United Fruit Company to eradicate the pathogen from certain areas in Central America. In this process banks are constructed around affected sites which are then flooded to a depth of 2–5 ft. for periods up to 18 months (Stover, Thornton & Dunlap, 1952). The pathogen, being strongly aerobic, dies out along with most of the other soil microflora, and Gros Michel replanted on such sites often remains healthy for many years. However, the dependence of this method on a flat terrain and an abundant water supply, together with the high cost of bank construction and pumping, greatly restricts the possibility of its application elsewhere.

As with other vascular wilts, the main progress with control is likely to come from the breeding of new resistant varieties. With the banana this is a slow and complicated business, increasingly hindered now by the fact that in recent years it has proved impossible to collect potentially valuable breeding material in South-east Asia. Meanwhile, perhaps the most important precaution to be observed in banana growing areas to-day is to try and ensure that soil structure and fertility are improved, or at least maintained, since further deterioration could lead to the appearance of wilt in varieties now regarded as resistant.

REFERENCES

Cronshey, J. F. H. & Barclay, C. (1939). Replanting in areas infected by root disease. *Arch. Rubbercult. Ned.-Ind.* **23**, 163. Reprinted in *Quart. Circ. Ceylon Rubb. Res. Sch.* **17**, 28.

Garrett, S. D. (1944). *Root disease fungi.* Waltham, Mass.

Hansford, C. G. (1926). The *Fusaria* of Jamaica. *Kew Bull. Misc. Inf.* 1926, p. 257.

Hartig, R. (1894). *The diseases of trees* (trans. by W. Somerville and Marshall Ward). London.

Leach, R. (1937). Observations on the parasitism and control of *Armillaria mellea. Proc. roy. Soc.* B, **121**, 561.

Leach, R. (1939). Biological control and ecology of *Armillaria mellea* (Vahl.) Fr. *Trans. Brit. mycol. Soc.* **23**, 320.

Murray, R. K. S. (1938). Root disease with special reference to replanting. *Quart. Circ. Ceylon Rubb. Res. Sch.* **15**, 24.

Napper, R. P. N. (1932–40). Observations on the root disease of rubber trees caused by *Fomes lignosus*, and other papers. *J. Rubb. Res. Inst. Malaya*, **4**, 5; and *Rep. Rubb. Res. Inst. Malaya*, 1932–9.

Petch, T. (1921). *The diseases and pests of the rubber tree.* London.

Rishbeth, J. (1950–1). Observations on the biology of *Fomes annosus*, with particular reference to East Anglian pine plantations. I–III. *Ann. Bot., Lond.*, N.S. **14**, 365; **15**, 1, 221.

Rishbeth, J. (1952). Control of *Fomes annosus* Fr. *Forestry*, **25**, 41.

Rishbeth, J. (1955). *Fusarium* wilt of bananas in Jamaica. *Ann. Bot., Lond.*, N.S. (in the Press).

Schoorel, A. F. (1949). *Handleiding voor de Theecultuur.* Wageningen.

Stover, R. H., Thornton, N. C. & Dunlap, V. C. (1952). Flood-fallowing for eradication of *Fusarium oxysporum* f. *cubense*: I. Effect of flooding on fungus flora of clay loam soils in Ulua valley, Honduras. *Soil Sci.* **76**, 225.

Wardlaw, C. W. (1935). *Diseases of the banana.* London.

Wiehe, P. O. (1952). The spread of *Armillaria mellea* (Fr.) Quel. in Tung orchards. *E. Afr. agric. J.* **18**, 67.

Doeksen, J. (1955). *Ann. appl. Biol.* **42**, 228–231

THE DEVELOPMENT IN RESEARCH AND CONTROL OF SOME IMPORTANT SOIL-BORNE INSECT PESTS

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In speaking of soil-borne insect pests, it is necessary to draw your attention to the complex of soil fauna problems as a whole. The soil, however, is a most difficult medium. In fact, we hardly know what 'soil' really is. Geologists, mineralogists, physicists, chemists, microbiologists, acarologists, entomologists and other zoologists claim to understand something of the soil and its problems, but as a complex it is only little known.

Manuring, not long ago, seemed to be a simple matter of adding a suitable form of nitrogen, potassium and phosphate to the soil. Now we know how easily the equilibrium in the soil can be disturbed. The available amounts of minor elements in many parts of the world are too low for the cattle fed on these plots, though the herbage does not show any signs of poor growth or damage. These problems now occupy many agricultural chemists all over the world.

Far more complex, however, is the soil fauna, which not only inhabits the soil, but is partly dependent on the soil for food. It is also affected by the vegetation, which in its turn depends on the soil, but of course in a different way.

It is only in the last 10 or 15 years that the study of the soil fauna has attracted more general interest. Before that time some biologists, such as Cameron and Morris, had been working only incidentally on this subject. Economically important insects, however, are now much studied and it would not be difficult to compile a list of 2000 publications on wireworms only. Yet in my opinion, the two main groups of soil animals, the pests and the harmless or beneficial ones, have to be studied as a whole.

A remarkable characteristic of the soil fauna is its lack of specificity. Parasites of soil animals are very scarce, predators are often abundant, but they are typically non-specific. This means that a high population level of the soil fauna in general will attract and maintain a dense population of predators. If in such circumstances one species multiplies beyond its normal numbers, a greater part of the attacking power of the predators will be directed against that particular species.

One of the most important characteristics of the soil is its buffering capacity, not only with respect to water and plant nutrients but also in relation to microflora, fauna and, last but not least, temperature. Therefore, compared with other habitats, the soil is very stable, but different soils show marked contrasts. Woods, generally speaking, form the best habitat for soil fauna. There is an abundant food supply which is available throughout the year and desiccation of the soil is largely prevented by the fallen leaves which shield the ground from direct sunlight. Orchards have a very well-developed soil fauna if mulching is practised; grass orchards are a less favourable habitat, and mowing the grass for hay decreases soil fauna to a very low level. The soil fauna of permanent grasslands is generally rich, unless the field is regularly flooded; but grassland used only for hay is very poor in soil animals. On arable land, most of the soil fauna is destroyed. I do not refer to 'A Plowman's Folly', for not ploughing would be far more foolish. Ploughing and harrowing is not directly fatal to soil animals, but the resultant shortage of food during part of the year, extreme temperatures, sudden changes in temperature and drought in the upper soil layer, due to lack of soil protection, will kill the greater part of the soil animals.

The study of soil fauna, be it of harmless and beneficial insects or of pests, is absolutely dependent on good collecting methods, and the fame of Rothamsted Experimental Station would not be what it is, if its staff had not studied this problem for 35 years, following the pioneer work of Morris. It is equally evident that where soil animals differ in size from 50μ to 35 cm., it is not likely that a single collecting method will be satisfactory for all animal groups. For a survey of the soil fauna as a whole, a number of extraction techniques will be necessary; for the study of special problems, one collecting method in most cases will be sufficient.

A triumph, in my opinion, was the development of the 'wet sieving-flotation-benzene-separation method'. I use this lengthy descriptive name on purpose, to show its development and to give credit to all who helped to develop it. Morris (1922) used a method in which he washed his soil samples over a number of sieves, collecting his insects by hand from them. Ladell (1936) broke down the coarser soil particles over a sieve, by stirring and the use of an air-jet and floated all the organic material on a salt solution, after which the animals had to be picked from the organic debris. Salt & Hollick (1944) combined the two methods but added benzene to the material floating on brine; the hydrophobic-animal matter collects in the benzene phase, whereas the plant material remains in the water phase. Cockbill, Henderson, Ross & Stapley (1945) applied this method in the practice of mass-sampling. By this method, we can now usually estimate the wireworm population of a field with a high degree of accuracy. But on coarse sandy soils, as we have in the Netherlands, it does not work very satisfactorily. So we had to devise other apparatus to do our mass countings of wireworms.

A very important survey was made in the years 1939-42 in England and Wales. It showed which parts of the country were generally most heavily infested, the south-east being extremely rich in wireworms. The same holds for our country, the Netherlands, though the differences are less pronounced, due, no doubt to the smaller distances. This 1939–42 survey is reported in a bulletin of the Ministry of Agriculture (1944) where is it suggested that there is a fairly definite association between number of wireworms and loss of yield in wheat and oats; we think there is a linear relation between crop damage and the square root of wireworm population density. The trouble, however, is that all these data only hold for averages, and that one cannot predict of a particular plot whether much damage will be suffered or not. But it is evident from the survey, that in cases of wireworm infestations, high seeding rates are often necessary for cereals. Flax and linseed, beans and peas are however little sensitive to wireworms, rape is only incidentally attacked by them; potatoes may suffer a severe loss of quality if used for human consumption; for animal food they can be ensiled after steaming and little loss of quality is noticed. I only once saw a potato field with a low yield due to wireworms, but in this case the crows had dug up the seed potatoes to get at the wireworms but had forgotten to replant the potatoes properly.

In 1944 and 1946, Salt and Hollick published the results of their very extensive and thorough studies on wireworm population. They found a significant or highly significant correlation between wireworm density and pH, loss on ignition, organic carbon and nitrogen in the upper soil layer. In practice, however, this correlation so far has never been found in the Netherlands, which was very puzzling. The explanation however is simple. There is a strong positive correlation between pH, nitrogen and water capacity, for good soils on the one hand and *Lolium perenne* on the other hand, but a strong negative correlation between ryegrass and wireworms. Now in practice, we seldom plough up an old pasture which is rich in ryegrass, therefore we never find the correlation mentioned by Salt & Hollick. Unluckily, however, it is only the click beetles and not the wireworms that dislike ryegrass, so in resowing grasslands either for leys or permanent pastures, the young grass may be damaged severely by the wireworms present.

As to the problem of ley farming, it is evident that in leys of good quality with much ryegrass, the building up of a wireworm population will be slow. On short-duration grasslands (4 years) of poor quality, however, wireworm densities will only be little lower than on old pastures.

Before 1945 we had not met with the blessings of chemical insect control in soils other than for special, very expensive crops. After the war however, H.C.H. (BHC) was found to be very useful as a soil insecticide; luckily its smell prevented its use on a large scale in practice. In seed-dressings the quantity of H.C.H. or of its active part, the gamma isomer, can be much smaller and its effect on soil fauna in general less devastating, but the great danger of good and cheap soil insecticides is that advisory staff and farmers may look upon their use as on an insurance premium, forgetting all other possibilities of preventing damage by soil-borne pests.

It is true that we soil zoologists cannot yet tell you exactly the value of soil fauna for the soil and its maintenance, but if the use of soil insecticides becomes a general practice, we shall not even have time to find out. New and better soil insecticides are on the market already. The chemical way of thinking is a danger to all applied biologists, but it is particularly dangerous in connexion with the soil, for chemical treatment may affect its most important characteristic, its buffering capacity.

The control of leatherjackets as it has been done for many years is an example of a specific control. By baiting them with poisoned bran, only a little harm is done to other faunal elements, but here also non-specific soil insecticides can be used and are used already on a large scale.

Here I want to call attention to the work on grubs, done by our Swiss and French colleagues, of whom I mention only Grier, Murbach, Bourqui & Pugnat out of many others. They show clearly the extent to which ploughing and harrowing can decrease the population density of grubs, viz. 75–85%.

Grazing grassland instead of mowing decreases grub populations by 53%. It is true that these measures tend to decrease soil population as a whole, but the populations can restore themselves rather quickly. This does not take place after the use of soil insecticides. By combining sensible soil cultivation, choice of crops and seed quantity, the use of soil insecticides can be restricted to incidental cases.

This kind of research is very important, for our knowledge of the biology of soil animals is only fragmentary. We should never forget that through agriculture we disturbed the equilibrium in nature and our task as biologists is not to try to aggravate this unbalance, but to find a way to adapt our agriculture to nature, restricting disturbances to the necessary minimum.

REFERENCES

Cockbill, G. F., Henderson, V. E., Ross, D. M. & Stapley, J. H. (1945). Wireworm populations in relation to crop production. I. A large-scale flotation method for extracting wireworms from soil samples and results from a survey of 600 fields. *Ann. appl. Biol.* **32**, 148.

Ladell, W. R. S. (1936). A new apparatus for separating insects and other arthropods from the soil. *Ann. appl. Biol.* **23**, 862.

Ministry of Agriculture and Fisheries (1944). *Wireworms and food production: a wireworm survey of England and Wales* 1939–42, pp. 62. London: H.M.S.O.

Morris, H. M. (1922). On a method of separating insects and other arthropods from the soil. *Bull. ent. Res.* **13**, 197.

Salt, G. & Hollick, F. S. J. (1944). Studies of wireworm populations. I. A census of wireworms in pastures. *Ann. appl. Biol.* **31**, 52.

Salt, G. & Hollick, F. S. J. (1946). Studies of wireworm populations. II. Spatial distribution. *J. exp. Biol.* **23**, 1.

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Kramer, L. M. J. (1955). *Ann. appl. Biol.* **42**, 235–246

THE APPLIED BIOLOGIST, THE CHILD, AND SOCIETY

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Consideration of the characteristics of past and current applied biology reveals its fundamentally ecological nature, and also indicates the potent influence of the applied biologist upon society. It is urged that in order to impress this influence upon pupils biological education should be based mainly upon field studies, rather than upon predominantly evolutionary, morphological and physiological studies. The nature of past and existing school biology strongly reinforces the above conclusion.

The results of attempts to find and evaluate evidence of the social influences of past and present biological education are presented, both in relation to the whole population, as well as to particular aspects, like food poisoning, the press, and the education of Civil Servants and Members of Parliament.

The potentialities of a Sixth Form biology resting chiefly upon field study are discussed not only as a means of developing an outlook valuable to-day, but also of treating suitably the pre-university education of future applied biologists.

Introduction

Society as a whole is growing accustomed to the kind of spectacular scientific changes which have occurred during the lifetime of our Association. Education, faced with the task of preparing a constant stream of children for life in such a changing society, has also certainly undergone striking alterations, and not least notably by expanding science teaching since its small beginnings in the nineteenth-century. Ninety per cent of the biology now taught in boys' Grammar and Public schools, for example, started during the last thirty years (Brown, 1953). Events have moved far beyond the time when biology teaching was almost entirely systematic botany, zoology was rarely studied, and practical work was held by some to demoralize pupils, who were supposed to accept without question all that their teachers uttered (Brown, 1953).

The problem of the biology teacher to-day is to discover how the special qualities of his spacious subject can be used to advance the general education of his pupils. And because it is clear that the application of biological science to human needs has influenced society as a whole, the teaching ought to include a balanced general account of these applications. Consequently, it is apparent that there is a connexion between the work of the applied biologist, of the biology teacher, and the child: both affect the child and, either through him or directly, also affect society. To appraise the role of schools, both in these broad educational aspects and in the guidance and selection of future applied biologists, it is necessary to study the nature and effects of applied biology and the scope and attributes of school biology.

THE NATURE OF APPLIED BIOLOGY AND ITS PLACE IN SOCIETY

The educationally fruitful aspects of applied biology are not the detailed points at issue in research or in advisory matters, so much as the wide general principles, of which one may cite three examples.

(1) The distribution of Neolithic and later sites of human dwellings, pollen analysis and the investigation of mud samples from the floors of lakes combine to show how areas like Breckland, Danish and German heaths, south-east English heaths and Dutch polders have been stripped of a once rich and often arboreal vegetation. From this study we can learn to avoid the errors of our ancestors and realize that by the application of sound ecological knowledge these areas may be restored to fertility (Pearsall, 1952).

(2) It was not until the nineteenth century that the physical state of humanity changed from one of constant threat of famine and pestilence. During the last 150 years, however, while some three-quarters of the world's population still faced a somewhat precarious state of food supplies, the remaining quarter, although often living far away from the chief food-producing areas, have come to enjoy freedom from famine and have been able to develop complex industrialized societies. This change has been really due to an elaborate study and application of ecological principles, for every major aspect of food production fits into the ecological pattern, from the relationship of rocks to soil types at one end of the interlocked chain of events, to the handling of food by those who consume it at the other (Scott Robertson, 1948; Russell, 1949; Fenelon, 1951).

(3) Again, we can follow how there has come about during and since the nineteenth century a change from a state of high mortality rates and short expectation of life, to one of longer lives, lower death-rates and an increase, still continuing, of world population. But the modern science of demography, developed from the handling of population records compiled at least in advanced countries, owes much to animal ecology, because it has been shown that the modes of growth of both animal and human populations, *in vitro* and in nature, are in general alike. Here again, one sees the ecological foundations of the significance of, and possibly even for the conscious control of, human populations, even if the application of knowledge is as yet neither universal nor as wise as it may one day become (Bodenheimer, 1953).

It is easy to elaborate the view that ecology is the basis of applied biology, there is no lack of evidence for it, and if it be conceded that this interpretation is correct, a certain biological structure of society can be discerned, one that is comprehensible to young people and which should probably form a part of their general education.

Mankind is irregularly distributed over the 7 to 10% of the land masses of the globe which are climatically or otherwise suited to provide sustenance. A relatively primitive majority support an industrialized, crowded and advanced minority. Man then appears as a world-wide biotic factor, for by his technological discoveries he has become able to colonize and use almost every type of habitat. Perhaps the most portentous feature of such a conception of human society is that because the scientific method carries within itself the means to increase knowledge and the control of the environment, man is more potent than any animal biotic factor.

If this reasoning is sound we have a clue to the true place of the applied biologist in society. Without him civilization in its contemporary form and on its existing scale, with its present power to avert the calamities common in the past and to develop a far more delectable future, assuredly could not survive. His place is incontrovertibly central. To convince ourselves of the truth of this we have but to ask what would happen if all applied biologists, both advisory and in research, were withdrawn from their work.

Furthermore, the ecological foundations of general and applied biology, and the realization of the paramount importance of applied biologists, seem to dictate the proper structure for biology in schools, suggesting that it becomes the duty of the biology teacher to enable his pupils to appreciate this outlook and its implications. With such thoughts in mind we may next examine the present state of school biology.

SCHOOL BIOLOGY TO-DAY

The high proportion of the teachers in Primary and in Secondary Modern schools who are certificated (about 84·4 %) have received a form of biological training, because Health Education is a compulsory subject in the examination for the Teacher's Certificate. Evidence exists (British Association Report, 1953) that the Teacher training colleges are trying to improve health education courses, which have hitherto been almost entirely theoretical. The bulk of our population passes through the Primary and the Secondary Modern schools, so that in them lies the largest field of opportunity for educational influences of all kinds. Evidence points to a considerable volume of some kind of biological work being carried on in these schools, although it tends to be rather 'academic' and could be related more closely to everyday life and greatly strengthened in field work (British Association Report, 1953).

Although good technicians may be recruited from Secondary Modern or Secondary Technical schools, it is almost always among those educated in Secondary Grammar schools (a term used in this paper to include Public and Independent schools), and who are therefore able to undertake University training, that one has to seek future scientists.

A major part of Grammar School work consists of the preparation of pupils for public examinations. Table 1 shows that between 1918 and 1950 the total number of candidates in the School Certificate Examination in England and Wales increased three times. Since 1950 the corresponding number has risen to 202,245 in 1953. During the same period the numbers of candidates in Botany fell greatly, Zoology ceased to be taken, but the numbers taking Biology rose from 2·5 to 31·5 % indicating a better balance between botany and zoology in the teaching and in fact a substantial increase in the animal biology taught, since the papers included questions on both zoology and botany. From Table 1 it can also be seen that at Ordinary (or 'O') Level in the General Certificate of Education ('G.C.E.'), equivalent to about the former matriculation standard, the bulk of the candidates in various types of biological subjects between 1951 and 1953 took General Science (which has a biological section with both botanical and zoological questions) and Biology. Thus the better balance between botany and zoology and the actual increase of zoology have been maintained (British Association Report, 1953; Ministry of Education Reports, 1951 to 1953).

TABLE 1. *Candidates in biological subjects*

				Averages for 1951 to 1953	
SCHOOL CERTIFICATE	1918	1950	G.C.E.	'O' LEVEL	
Total candidates	33,563	99,883	Total candidates	166,119	
Percentage entry for:			Numbers entering for:		
General Science	—	—	General Science	23,226	
Additional General Science	—	—	Additional General Science	3,050	
Botany	25·2	1·3	Botany	754	
Zoology	1·3	0	Zoology	48	
Biology	2·5	31·5	Biology	34,328	
Agricultural and Horticultural Science	—	—	Agricultural and Horticultural Science	262	
Chemistry	—	—	Chemistry	25,616	
HIGHER CERTIFICATE			G.C.E.	'A' LEVEL	'S' LEVEL
Total candidates	1,303	34,364		40,689	—
Percentage entry for:			Numbers entering for:		
Botany	6·2	8·7	Botany	3,016	871
Zoology	0·46	8·47	Zoology	3,167	1,011
Biology	0·54	9·8	Biology	4,393	1,118
Chemistry	—	—	Chemistry	13,732	3,868

For comparison one may note that the numbers of candidates at 'O' Level in chemistry were not as numerous as those in biology, although very often candidates in biology also enter for chemistry and physics.

Therefore it appears that in the Grammar schools the biggest field of influence in biology is among the candidates in General Science and in Biology, and although this field is important, it is numerically much smaller than that in the Primary and Secondary Modern schools.

In the Higher Certificate Examination the total number of candidates increased between 1918 and 1950 about 26·4 times (Table 1), and has risen since then to a corresponding figure of 44,909 in 1953. The changes in the numbers of candidates in biological subjects showed a great increase in zoology, both when taken as such and as a component of Biology. In the G.C.E. at Advanced (or 'A') Level and Scholarship (or 'S') Level between 1951 and 1953 the relative proportions between the numbers of candidates were chiefly similar to those in the Higher Certificate in 1950 (British Association Report, 1953; Ministry of Education Reports, 1951 to 1953).

The candidates in Chemistry at 'A' and 'S' Level appear to outnumber those in biological subjects, but it is usual for the latter to take Physics and Chemistry.

The development of school zoology in the past thirty-five years can also be seen from the greater range of types of animals mentioned in various contexts in the syllabuses of the Examination Boards (Brown, 1953), and from the figures in Table 2 which show the numbers of animals sold to schools by a prominent dealer.

TABLE 2. *Sales of laboratory teaching material*

(After Brown, 1953)	1919	1950
Dogfish	100	12,000
Rabbits	50	5,500
Rats	0	1,620

A closer insight into the kind of biology covered can be obtained by inspecting the syllabuses published and the questions set upon them by the Examination Boards. Three of the eight boards in England and Wales examine between them 65·5 % of all the candidates (The Oxford and Cambridge School Examination Board, The University of London, and the Joint Matriculation Board of the Universities of Manchester, Liverpool, Leeds, Sheffield and Birmingham).

In General Science and Biology at 'O' Level the syllabuses of each of these three boards give a good lead in field study, either by a general directive or by specifying habitats which are to be studied. The syllabuses vary in the extent to which they refer to applied biology. In General Science a wide range of topics is mentioned: errors of refraction of the eye, diet, infectious diseases, carbon monoxide poisoning, crop growth, grafting and budding, parasitism, food preservation, insect pests, etc. In Biology, the Oxford and Cambridge Board give a good lead, but London and the Joint Matriculation Board are not so specific in their references.

In Table 3 is a summary of the analysis of 547 questions set by the three boards in fifty-seven papers. A 'reference' here means the mention of a topic or a clear indication from the wording of a question that a certain topic or organism had to be discussed. One question may specify several organisms or topics, so that analysis by 'references' is more comprehensive and detailed than by classifying whole questions. As an example of the results one may note in Table 3 that 7·1 against spore plants means that 7·1 % of all the references were to those plants.

The following points emerge:

(1) The lead concerning field studies and applied biology in the syllabuses has been certainly followed up by making a certain proportion of references to them in the questions.

(2) By adding together the figures for references to seed plants and mammals (32·04 + 34·45) it is found that 66·49 % of all references were to those subjects.

It was therefore quite possible for a candidate to acquit himself well at 'O' Level by answering only the parts of papers which referred to seed plants and mammals.

At 'A' and 'S' Levels the syllabuses of the three boards usually give a general directive about field studies and in regard to applied biology usually name relevant topics or organisms. The Joint Matriculation Board's Syllabuses cover field studies more fully than do those of the other two boards, while the Oxford and Cambridge Board set out references to applied biology more fully than do the Joint Matriculation Board or the University of London. In general, the zoological syllabuses cover these two branches of study more elaborately than do those for botany.

TABLE 3. *Analysis of questions set in General Science and Biology in G.C.E. Examinations at 'O' Level*, 1951–53

Subjects	Average percentage of total references
Spore plants	7·10
Seed plants and plant physiology	32·04
Invertebrates	4·68
Vertebrates (excluding mammals)	2·52
Mammals and mammal physiology	34·45
General biology	5·12
Field study	3·37
Applied biology	9·50

A preliminary analysis of the questions set upon these 'A' and 'S' Level syllabuses indicates that an average of 49·9% of references were to the anatomy and morphology of organisms. The lead given in the syllabuses to field study and applied biology was followed, for the references to each of these branches averaged 5·6%. On this evidence one may suggest that a candidate who confined his answers to anatomy and morphology may have acquitted himself fairly well; but a full analysis of questions may point to a different conclusion. The sources of information consulted in connexion with these studies of 'A' and 'S' Level syllabuses and questions are the same as for those given above for 'O' Level.

Taking into account the powerful case for field study and the ecological approach as the proper basis for school biology in general, and as the means for producing a vivid understanding of the significance of applied biology, and bearing in mind the aspects of school biology revealed by investigations of syllabuses and questions, there would seem to be good reasons for re-aligning much of school biology upon the foundation of ecology, rather than upon anatomy, physiology and evolutionary studies.

This conclusion is strongly supported by evidence cited in published criticisms of Grammar school biology (Kramer, 1949; British Association Report, 1953), suggesting that it is tied too much to text-books, and neglects the study of living material and of field work. Moreover, it is still quite possible for a candidate at 'A' and even 'S' Level to pass well in biological subjects without having done any biological work outside of classrooms or laboratories.

But ways to improve matters do exist. Her Majesty's Inspectors of Schools, an awareness of the problems in Teacher Training establishments, and the steady increase in the numbers of those attending the Council for the Promotion of Field Studies' Centres are all potent influences. The vigorous Science Masters' Association provides useful reading matter for both teachers and pupils. In its periodical, the *School Science Review*, there have appeared since 1949 fifteen articles on school ecological work and on aspects of applied biology, while out of 1825 titles of books in their list advised for stocking school libraries there are 190 on natural history, 31 on applied biology and 68 on agriculture (*School Science Review*, 1949 onwards; Science Masters' Association, 1949).

THE INFLUENCE OF SCHOOL BIOLOGY

There are a few clues to the influence of school biology upon the community. In Table 4 are figures which show the numbers of young persons who, as candidates in the G.C.E. Examination at 'O', 'A' and 'S' Levels, have some biological background. They are added to the population each year and form the percentages of it shown in the table. In many schools there are courses in science for Sixth Form students of the humanities. Questions on biological subjects are set in the General Papers for candidates for Entrance Scholarships in the humanities at the older universities, although the colleges vary much in this respect (see Cambridge University Press Papers, 1950 onwards).

TABLE 4. *Approximate numbers of persons newly qualified in biology each year*

	Actual numbers	As percentage of population of England and Wales
G.C.E. Biological candidates at each level:		
Ordinary	57,554	0·1300
Advanced (Biology)	4,393 (minimum)	0·0099
Scholarship (Zoology and Botany)	1,882 (minimum)	0·0043
Advanced and Scholarship ($=X$)	6,275	0·0140
Newly registered medical practitioners [before 1953] ($=Y$)	4,493	0·0100
Sixth Form pool ($=X-Y$)	1,782	
New members of Association of Applied Biologists	55	0·0001

But in 30% of the boys' Grammar schools over half the pupils leave without receiving any formal biological education (Brown, 1953). The implications of this are apparent when we bear in mind the positions of influence which Grammar school pupils so often attain in later life.

The increase in school biology in the last 30 years has coincided with a steady rise in the number of cases of food poisoning, (British Broadcasting Corporation, 1954). It is legitimate to ponder whether a people educated adequately in biology would tolerate such an increase of a complaint whose causes and channels of infection are known and which is theoretically preventable by laymen. In fact, active measures are being taken to remedy matters, including suitable courses for children about to leave school, and for persons engaged in the food industries. Perhaps there are relationships between the quality of biological education and other social phenomena like infestations of persons by lice or the scattering of litter in public places. An attempt to discover reliable evidence might be worth while.

The general public obtain some information on biological matters from the press, but their treatment varies much in regularity and quality. The figures in Table 5 have been obtained from a study of 1 day's issue of *The Times*, *The News Chronicle*, *The Daily Herald* and *The Daily Mirror*. On that day, 6 July 1954, there was an average of 5·5 biological references in each paper. The categories of biological subjects discussed, in order of frequency, were: natural history; miscellaneous topics hard to classify; agricultural, economic or industrial matters; sporting matters.

TABLE 5. *Biological and medical references in 1 day's issue of four daily newspapers*

	Number of references	
	Total	Average
In text:		
Biological	29	7·25
Medical	16	4·00
In advertisements:		
Biological	30	7·50
Medical	13	3·25
Total	88	22·00

Excluding the Judicature, members of the House of Lords and of the House of Commons, the sixty departments of the British Government, as constituted in June 1954, comprised down to the level of Assistant Secretary 1660 senior Civil Servants, many of whom are presumably concerned with the formulation of policy or the preparation of legislation. Bearing in mind that the published lists of these names may not give all who have scientific qualifications (Vacher, 1954), it is, however, found that 58 (3·5 %) of the 1660 are stated to have scientific qualifications, and 7 (0·42 %) appear to be biologically qualified. Of course some departments have large and well-qualified scientific staffs and inter-departmental co-operation is possible, but one can contend that what may matter is the ability of the general administrator to recognize and to see the implications of public affairs of a biological nature, and that his education in this respect may be worthy of review.

In attempting to analyze the biological qualifications of Members of Parliament, a 20% sample, consisting of 125 names, was obtained by marking every fifth name on the alphabetical list of members of the House of Commons as constituted in June 1954 (Vacher's list). Each member in the sample was then looked up in *Who's Who*. The material point is that if a member has a really keen interest, connexion or hobby, he is likely to mention it in *Who's Who*. It is, however, obviously necessary to treat such evidence cautiously. Yet even with this reservation, the analysis displayed in Table 6 indicates that with the figures quoted as very likely to be minima in each category, the numbers of members having qualifications of a category likely to inform judgement on biological matters of national significance are certainly meagre.

TABLE 6. *An estimation of the biological qualifications of Members of Parliament, June* 1954

	Numbers in sample	*Pro rata* in whole House	As %
Total	125	625	100
Having biological connexions	38	190	30·4
Subdivision of these 38:			
A. Biologically qualified	0	0	0
B. Qualified in other sciences	2	10	1·6
C. Medically or dentally qualified	7	35	5·6
D. Farmers, or have worked on farms	5	25	4
E. Having biological interests (e.g. business)	4	20	3·2
F. Having agricultural interests	7	35	5·6
G. Having a biological hobby	13	65	10·4

SIXTH-FORM BIOLOGY AND THE FUTURE APPLIED BIOLOGIST

It is not nowadays necessary to plead for some appropriate biological teaching for all before the school leaving age or before the sixth-form level in Grammar schools. The subject, made cogent by the work of applied biologists, is as desirable an ingredient of school life as history or languages, and if omitted from school science will leave larger gaps in mental equipment than if chemistry and physics are left out.

At the Sixth Form stage, however, some specialization perhaps inevitably occurs and the question then is what should be the proper attitude to, and the purpose of, the biological work, not only as an educational medium in its own right, but also as preparation of future professional men, including biologists.

At the Inaugural Meeting of the Jubilee Conference of our Association distinguished guests from abroad paid generous tributes to the quality of British work, from which one may justifiably believe that our educational bases are sound. But there is always room for stocktaking, and I have outlined the present situation and made suggestions, based on evidence, which might both balance presentation better and enhance the effectiveness of the subject.

In Table 4 are figures which show that an average of at least 6275 candidates sit each year at 'A' and 'S' levels in the G.C.E. in biological subjects. In 1952, 4493 new medical practitioners were registered, representing a replacement rate to the medical profession of 5·4%. If we take the membership of the Association of Applied Biologists as a rough guide to the numbers of applied biologists, the average number of new members for the years 1951–53 was 55, representing a replacement rate of 8·1%. On the quite fair assumption that the newly registered medical practitioners were formerly members of Grammar school Sixth Forms, we have a pool of about 1782 (i.e. 6275–4493) Sixth Form members available each year to enter non-medical careers in biology, and quite ample to replenish the Association of Applied Biologists. In view of the central position of applied biologists in human economy, their ratio to the whole population is noteworthy as compared with that of doctors: there are approximately 75 doctors to every applied biologist.

The problem thus appears to be resolved into how the schools should treat the non-medical biological pool for whom careers as biological scientists will vie with others like pharmacy, veterinary work, agriculture, etc., and from among whom there will be diversion into non-biological careers.

It is axiomatic that as far as possible schools should provide general, not vocational, education. Unless a pupil becomes a teacher, and even if he becomes a professional scientist, he will forget anatomical and much other detail in a few years. Consequently, the task over the school years is so to devise the approach to the subject that a suitable impression is left in the mind in after years. To produce this, time is needed, both during and after school life. Now, Sixth Forms are perhaps a British educational invention and are permeated by a jealously guarded tradition. They offer sound scholarship in the widest sense, develop habits of accuracy in thought and presentation and provide intellectual discipline.

If biology is to look other disciplines squarely in the face, so to speak, it must at least equal them in these types of educational possibilities. What then are its claims as a Sixth Form discipline? Like physics and chemistry it gives opportunity to develop manual skill. But it provides a different outlook from them on natural phenomena, and therefore one with a broadening effect on the mind, because of the nature of biological conceptions of time, of precision and of the behaviour in the widest sense of whole organisms and whole populations.

If there are sound theoretical reasons for the practical study of biology in the field as not only the proper basis for school biology, but also to vivify it, there are indeed compelling practical reasons as well. One has but to see the effect upon a class of a surfeit of indoor laboratory and theoretical study as compared with the effect of an enthusiastic and imaginative approach out of doors, to the 'science of scenery' to be convinced of the absolute soundness of this view. To amplify the point one may list the ways in which field study furnishes examples of nearly all the applications of biology to human needs:

(i) The relation of topography and rocks to soil types.

(ii) The relation of soil types to vegetation and therefore with (i) to landscape.

(iii) The nature and types of plant nutrition.

(iv) The types of predators, of parasites and of symbiosis.

(v) The role of animals, fungi and bacteria as agents of decay and as the prime movers in the circulation of substances.

(vi) The food chains and the bases of animal nutrition.

(vii) The types of reproduction, studied as an introduction to genetics.

(viii) The structure and ontogeny of plant and animal communities, including the behaviour and mental phenomena of animals.

All this can be studied with relatively little and inexpensive apparatus and forms the best starting-point for complementary laboratory anatomical and physiological work. Indeed it sets the laboratory and its equipment in a correct perspective, shifting it from the central place into the position of an essential tool for the study of the organisms seen in the field. But the chief educational significance of biological field studies probably lies in their triple nature. First, there is the science of ecology, with its own principles, providing an intellectual discipline of great possibilities. Secondly, there is contact with nature as a means to kindle the emotional aspects of life so important in education. And thirdly, we can develop the first two qualities of biology by using observable facts of nature *and* of current rural and urban life. A great deal of our national activity is necessarily based upon industry, commerce and cities and thus is bred an urban outlook. To change this outlook is almost impossible. It is probably best to try to use the unique qualities of biological education to deepen the personality in several directions, and to attempt to provide, for maturation in later years, a trained intelligence and a sensitiveness to the arts, from which combination there is at least the possibility of the growth of an underlying spiritual satisfaction. For without that satisfaction, no one can acquire the wisdom to apply any of our science aright.

The author dedicates this work to his wife with earnest thanks for her co-operation during a critical period, thus enabling the paper to be produced in time for the Jubilee Conference.

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REFERENCES

Bodenheimer, F. S. (1953). On animal and human populations. *Sci. News, Harmondsworth*, **30**, 43.

British Association for the Advancement of Science (1953). Biological sciences in British schools. *Advanc. Sci., Lond.*, **37**, 1.

British Broadcasting Corporation (1954). Food Hygiene, 12 January 1954.

Brown, E. S. (1953). Zoology in the schools, 1851–1951. *Sch. Sci. Rev.* **125**, 71.

Cambridge University Press (1950 onwards). *Examination papers for scholarships and exhibitions*.

Fenelon, K. G. (1951). The world's food supplies. *Advanc. Sci., Lond.*, **29**, 26.

HER MAJESTY'S STATIONERY OFFICE (1954). *Registrar General's estimates of population of England and Wales*, 1954.

JOINT MATRICULATION BOARD (1953*a*). *General Certificate of Education, regulations.* Timperley, Cheshire, England: John Sherratt.

JOINT MATRICULATION BOARD (1951, 1952, 1953*b*). *Question papers, General Certificate of Education, Advanced and Scholarship levels.* Timperley, Cheshire, England: John Sherratt.

KRAMER, L. M. J. (1949). Some aspects of sixth form biology. *Advance. Sci., Lond.*, **21**, 33.

MINISTRY OF EDUCATION (ENGLAND AND WALES) (1951, 1952, 1953). *Education in* 1951, 1952, 1953. London: H.M.S.O.

OXFORD AND CAMBRIDGE SCHOOLS EXAMINATION BOARD (1953*a*). *Regulations for Certificate Examinations.* Cambridge University Press.

OXFORD AND CAMBRIDGE SCHOOLS EXAMINATION BOARD (1951, 1952, 1953*b*). *Question papers, General Certificate of Education, Ordinary, Advanced and Scholarship Levels.* Cambridge University Press.

PEARSALL, W. H. (1952). Habitat, vegetation and man. *Proc. roy. Instn G.B.* **159**, 410.

RUSSELL, E. J. (1949). World population and world food supplies. *Advanc. Sci., Lond.*, **23**, 173.

SCIENCE MASTERS ASSOCIATION (1949). *Science books for a school library.* London: John Murray.

SCHOOL SCIENCE REVIEW (1949 onwards). A variety of biological articles. *Sch. Sci. Rev.* **111** to **127**.

SCOTT ROBERTSON, G. (1948). Agriculture and the world food problem. *Advanc. Sci., Lond.*, **19**, 65.

UNIVERSITY OF LONDON (1953*a*). *Regulations for the General Certificate of Education.* London.

UNIVERSITY OF LONDON (1951, 1952, 1953*b*). *Question papers, General Certificate of Education, Ordinary, Advanced and Scholarship Levels.* London.

VACHER AND SONS Ltd. (1954). *Parliamentary companion*, no. 904. London.

Brown, W. (1955). *Ann. appl. Biol.* **42**, 247–252

TRAINING IN APPLIED BIOLOGY AT THE UNIVERSITIES

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The training of applied biologists at the university level will vary considerably according as the student is primarily interested in the botanical or the zoological side, and there is no doubt a great deal of diversity on methods of training at the different universities. Any attempt to review, and still more to evaluate, the various methods in use would be difficult and dangerous, and in fact I can claim no extensiveness of knowledge in these matters. The following account will therefore be limited, in the main, to personal experience, which derives from a fairly long spell of botanical teaching at the Imperial College of Science and Technology. Certain features of the teaching at that Institution, at any rate as concerns undergraduates, are traditional, going back to the time of Huxley; others have been modified or have been introduced to meet changed conditions. Inasmuch as I have applied these methods throughout my teaching career, it may be assumed that I am in general agreement with their usefulness, but I would be the last person to suggest that these methods are necessarily right and that all others are wrong.

I shall begin with the intake of students. What stage have they reached, not merely in biology but in other subjects, at the time of entry? What type of student do we hope to find in a new entrant? I shall then take up the general content and arrangement of the undergraduate course, and deal finally with postgraduate research.

Thirty or forty years ago only a small minority of men entering college had had any previous formal training in biology. But a change had already begun. Here and there biology had entered the school curriculum, largely under the inspiration of certain science masters, but from about the end of the First World War biology has gradually established itself as one of the standard school disciplines, on the same level as, say, mathematics or chemistry or the classics. Over much the same period there has been a further change and one which has affected all subjects; namely, the gradual taking over by the schools of all teaching up to Intermediate level. Both these changes have led to important effects upon university teaching.

First, as regards the more general effect. The modern student is on the average about 2 years older when he begins his university course than was his predecessor of 30 years ago, i.e. 18–19 as against 16–17. He has already completed his Intermediate (or equivalent) training and, with the general abolition of the Intermediate year at the universities, possession of this qualification has now become a necessary condition of entry. At Imperial College abolition of the Intermediate year did not in fact come about until after the Second World War. Though its importance had dwindled over a number of years it was kept alive by the particular needs of some departments and by the very uneven standard of preparedness shown by entrants in the years immediately following the close of the last war.

The change as affecting biology may now be examined. The old-time freshman who intended to specialize in a biological subject (and who indeed in a number of cases changed over to biology from another subject in his second year) joined the Intermediate year, which comprised courses in mathematics, applied mathematics, physics and chemistry. He did not enter the biological departments until his second year. As most of the students had had little or no previous biological training, the first courses in botany and zoology were of an elementary character, aiming at giving a general picture of the subject. The more specialized work then occupied most of the remaining 2 years of the course. As time went on however, the proportion of students with some experience in biology increased, and what was more important, the standard of their attainment was higher. This was true especially of laboratory training; a student in the earlier days might possess a fair text-book knowledge of the subject but his experience of practical work was often of the slenderest. It was inevitable that progress along these lines should take place at different rates from one school to another, with the result that, for a time, there was great inequality in the members of the elementary course and, it may be added, it was next to impossible to devise a course suitable for such a mixed group. In due course there was a levelling-up in the schools, so that in recent years it has been possible to abolish the old elementary botany class, so far as students proceeding to honours in botany are concerned. The present-day student in botany at Imperial College, begins his botanical study in his first year, proceeding straight to more advanced work, apart from a 'settling down' period of a few weeks in the elementary course.

I have outlined the above series of changes, largely to draw an important conclusion. The higher degree of training shown by the modern entrant to a university has meant earlier specialization. This now takes place at about the age of 16 when the pupils at school are sorted into two main groups: those who are aiming at being chemists, physicists, engineers, etc., and who go on to Intermediate standard in mathematics, physics and chemistry; and the other group which includes the future agriculturalists, medical doctors and biologists, who specialize in biology (or botany and zoology) with one or at most two of the physical sciences. Generally the subjects dropped by the latter are mathematics and often also physics. The almost invariable result is that the biological student is inadequately grounded in physical science, a lack which is not always due to inability to cope with that subject. Now, as everyone knows, the modern trend in biological research is towards the physiological, which in turn is becoming more biochemical and physico-chemical. Hence it can be strongly urged that the advance in biological training at school, while it has everything to recommend it as bringing valuable knowledge to the general citizen, is definitely not to the advantage of the budding professional biologist. His biological training at school has been obtained at the expense of further training in the mathematical-physical sciences, and it is fairly probable that he will never be able to repair the loss.

Considerable interest attaches to the reasons which lead a student to choose a career in a biological science; hence the importance of interviewing prospective entrants. Why does he wish to take up, say, botany? What is his interest in plants? What experience has he had so far with plants? And so on. The answers are various. On the one hand there is the boy who has all along been interested in plants; who has collected and identified them; who has made a habit of working in the garden or on a farm; who even reads the gardening and farming journals. Very much at the opposite end of the scale is the boy who tells you that an older boy from his school had gone up to a university, had taken a degree in botany and had given a talk to their science club. It had all been very interesting, and that was what had made him think of botany. In the light of such information and of the candidates' academic record it is usually possible to decide who are the likely ones and to make one's choice accordingly.

As to the content of the undergraduate course (for Honours B.Sc.) there is no need to embark upon details. One aims at covering the botanical field in a general way and special parts are enlarged upon according to the interests of the teacher and to some extent to the traditions of the institution. Thus plant physiology and mycology-plant pathology have been for many years leading topics of the botanical course at Imperial College. With the passage of years room has had to be made for new or rapidly developing subjects, e.g. cytology and genetics, and this has been arranged by a certain amount of pruning of the traditional courses in morphology and taxonomy, partly also by the almost complete abolition of the elementary course, to which reference has already been made. There is no doubt that this re-orientation has gone farther in some university departments than in others and obviously there is room for varied opinion as to the balance to be aimed at. Though an expert knowledge of the whole subject is no longer possible to any one person—the term 'general botanist' can now be used only in a very qualified sense—it still seems desirable that a student should obtain a view of the subject as a whole, if for no other reason than that it helps him to decide what part of it is specially interesting to him.

Without much doubt the most important item in a university course in biology is the opportunity for practical work; after all, much of the material of lectures can be got by judicious reading in a good library. A peculiar feature of the courses at Imperial College is that they are given in concentrated form, that is, for perhaps a whole term a class is occupied solely with one branch of the subject, or nearly so. There is in this some risk of boredom, but on the other hand there is the supreme advantage of continuous practical work, which is especially important where the study of living organisms is concerned. Thus in cultures of micro-organisms it is possible to carry out fairly elaborate and lengthy experiments involving a connected series of observations and measurements. By this means the student gains not only a facility in handling organisms but also, as he is encouraged to develop his findings, he obtains some insight into research methods.

A further arrangement, also traditional, is the association of botany with zoology and geology, and until quite recently all students in botany took courses in the other two subjects, using one or the other for subsidiary (ancillary) purposes. Zoology still remains the usual ancillary subject for botanists, but the old-time link with geology has had to be weakened in order to find time for more chemistry. In view of the paramount necessity of further chemistry for all types of physiological research, geology has given place to special courses in physical-chemistry and biochemistry.

Practical work in the open, i.e. apart from collecting and identifying material or making isolated records, is usually not easy to arrange if this involves continuous observation of a growing crop. It is in this respect that the botanical undergraduate, as a potential applied biologist, is at a disadvantage compared with the student of horticulture or agriculture. Broadly speaking, the former has had the opportunity to be well grounded in basic principles but he is likely to be very deficient in the 'know-how' of cultivating and handling crops; the latter knows the details of culture, the merits of the various cultivated varieties, and so on, but is probably weaker in the basic sciences (physics, chemistry *and* biology)—obviously so, because of the large number of subjects in his curriculum. It is generally considered that the agricultural college type of training is better suited to the production of advisory officers and that a degree in pure science is the proper qualification for the research worker. There is no doubt a measure of truth in this though it would be easy to point out exceptions, both ways. In any case it must always be advantageous for the biological and especially the botanical student, if he intends to become an applied biologist in agriculture or horticulture, to miss no opportunity of becoming acquainted with the day-by-day routine of growing plants. For this purpose he should be encouraged to spend a large part of his vacations at one or more of the research stations or on the farm itself. In the time available he would hardly gain more than an inkling, but it would be a beginning, and if at the end of it he was still a long way from being an expert grower he would at least have some understanding of the kind of activities into which his future research work would be expected to dovetail.

The crisis of the undergraduate phase is the final examination, leading to the award of a degree of appropriate grade. This gives an assessment of the man's ability to assimilate information and to present it quickly in a convincing form. It does not follow that this is necessarily a true assessment of his potentiality as a research worker. As a convenient standard it is usually taken that a First Class or upper Second Class Honours degree is necessary for the man who wishes to go on to research and that below that level he would be unlikely to make good—again a rule which fits the majority, but allowances should always be made for exceptional cases. Perhaps the greatest objection to assessment by results of examination is a psychological one. The student, with an eye on examinations, may come to believe that a mind well packed with facts and second-hand opinions is the important thing and that so equipped he is complete and thoroughly prepared for his life's work. Education at the university level should be something quite different. Its purpose is to develop the student's innate capacity for thinking, so that with a reasonable background of factual knowledge he may be able to deal with problems as they arise and, in the case of the applied scientist, to make an intelligent use of the scientific method. For this purpose he will almost certainly have to acquire a new set of facts as he goes along. The capacity to discover one's facts, then, is the important thing, and not any particular body of facts. Viewed in this light the long and intricate discussions on what should or should not be included in the syllabus for such and such a degree are somewhat lacking in realism. Essentially the same result can be got from widely different syllabuses.

It is impossible, within the three or four years of undergraduate course, to give any adequate instruction in research methods. After all, the best way to learn research is to do it, and so the period of postgraduate training is essentially taken up with research. Some further class work is often desirable, for example to acquire special information or to become familiar with special techniques. Formal course work, and still less formal examinations, should no longer be required. It is the student's business to select and to seek out the kind of information which is likely to be valuable to him in the development of his research. Independent reading and general initiative are now expected of him.

The research topic, which it usually falls to the supervisor to suggest, may be academic or applied. Once upon a time it was generally held that the special function of universities was to work for the advancement of pure knowledge, whereas the research institutes were concerned with the application of knowledge to practice. Nowadays this distinction is more than a little blurred. Much applied work is being carried out in university departments and conversely much fundamental research in research institutes. The tendency in the latter respect seems to be becoming more pronounced. With more liberal equipment at their command, both in men and materials, many research institutes are in a much better position to promote fundamental research than are many university departments. One sometimes wonders whether a time is coming (if it has not already come) when the function of universities is merely to shepherd the research worker through his apprenticeship, and to be content with the preliminary sort of research which that is likely to produce, whereas the real substantive research, both fundamental and applied, will fall to the share of the research institutes.

The contribution of academic to applied research has already been discussed by Prof. Wigglesworth in the course of these meetings. With all that he said in that masterly lecture I heartily agree. I would merely like to add some remarks on the practice which I have adopted in allocating problems to beginners in research. As far as circumstances permitted I have aimed at giving each student two problems, one of an applied and the other of a fundamental nature. An applied problem in my subject (plant pathology) tends to be seasonal, requiring more or less full-time attention over part of the year; the fundamental problem often is such that it can be worked at at all times and also be laid aside for a period, without serious dislocation. It is then left to circumstances to decide whether both should be developed, and if only one, whether the applied or the fundamental. With the best students, it has often happened that both lines expanded so much that one of them had to be delegated to another worker. A material advantage to the student arising from this double venture is that it gives him a double chance of obtaining concrete results within the time normally available to him. The greatest advantage however is to the laboratory as a whole. Academic and applied research is in progress side by side and the one reacts upon the other; the former, inasmuch as it means an originality of approach and a fineness of method, stimulates the outlook and tones up the technique of the whole body of students; the applied work has at least a salutary effect in keeping the research from becoming too remote and as often as not it furnishes valuable pointers for fundamental study.

In due course there is the preparation of a thesis, and later the printed version. How much the supervisor should contribute to the writing up of results, as also to the direction of the student's research, is a moot point. Not too much nor too little would seem to be called for. The student who requires continuous help is not likely to go far, but on the other hand it would be tragic to allow a student to sink into a morass. As for the writing of a thesis, the novice, unless he be of exceptional ability, cannot be expected to view his work with a detached eye and present it in something like correct proportions. The technique of presenting results, like the technique of experimenting, has to be learned and the supervisor and student are equally concerned in seeing that the written account is a properly sifted and balanced statement of experiments carried out and of the results claimed from them. Incidentally the supervisor gains materially in the process. He sees, probably for the first time, the student's work in all its detail; he can judge for himself what quantity and quality of evidence there is for each conclusion drawn, and thus decide which parts of the problem have been rounded off and which will call for further investigation. On this basis he will plan the work of later students.

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BIOLOGICAL EDUCATION FOR AGRICULTURAL RESEARCH

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Whilst the universities rightly maintain that their teaching should be broadly based and free of vocational bias, university professors cannot help glancing over their shoulders at the world outside in an attempt to assess the trends in the market for their products. Now that the parental capacity to support a young man after graduation has almost vanished, it is essential that every graduate should earn his own living as quickly as possible and he and his parents are apt to consider it his professor's duty to provide the means for him to do so. To meet this pressure the professor must have a knowledge of possible openings for the men he is teaching in order that whilst he aims at giving a sound intellectual training he can direct the student's interests towards those aspects of his work which may be more likely to provide his postgraduate bread and butter, with even a hint of 'jam tomorrow'.

It is the object of this paper to try to set out those interests in biology, which if fostered will increase the young graduate's chances of fitting into the Agricultural Research Service.

The first difficulty is to define the boundaries of agricultural research. No human activity calls on a wider range of scientific disciplines for its study; nor on a greater breadth of approach within each discipline. Moreover, it calls increasingly for the services of men trained in more than one science for an attack on many of its most intriguing problems, and its continuously shifting demands require adaptability and versatility in the research worker.

The simplest approach is to start from the farm and to ask ourselves, what is the function of agricultural research in relation to it? It is to improve the means of production of food and other raw materials and in particular of those most wanted, which may mean either that we do not know how to produce enough or that we can only do so at a prohibitive cost. Its study must therefore include all means of increasing output and at the same time ways in which the input of labour and materials for each unit of production can be effectively reduced. We can approach these problems in two ways; the one by trying to overcome the difficulties well known and recognized by the farmer, the other by studying the methods of production from without in order to see where scientific knowledge can improve the existing techniques. A good example of the first method is the work which has been successfully completed on the control of red spider in commercial orchards, whilst the introduction and development of selective herbicides well illustrates the second.

The approach to agricultural research from the farm, however, tends to overemphasize the importance of applied and *ad hoc* research. Such problems can only be solved by the application of existing scientific knowledge, and it is one of the responsibilities of agricultural research to ensure that as far as possible this knowledge is available to the applied worker. Much of this background information is already available; independent workers in the universities are continually adding to it, but there still remain large gaps which must be filled; it is to do this that much fundamental research is carried out in the agricultural research institutes and subsidized in the universities by the Agricultural Research Council. Not only therefore does agricultural research need men trained in many scientific disciplines and of great breadth within the individual subjects, but it also calls for many types of research workers, from those who are happiest attacking fundamental problems in the seclusion of the laboratory to those who find their *métier* in carrying out field experiments working closely alongside the farmer and his men.

There is a tendency to regard the applied worker in the field as belonging to a lower order and what he does as hardly justifying the name of research. This is an entirely false assessment. It is true that the great scientific discoveries begin in the seclusion of the laboratory; it is there that the Nobel Laureate is bred, but it is equally true that much of the work which is classed as fundamental because it has no practical value, and probably never will have, is no more than competent hack work. On the other hand, applied problems in the field often call for research ability of a high order.

Research has been defined as the systematic search for knowledge, but this definition is incomplete unless we place limits on the knowledge which we seek. We may seek knowledge for two justifiable reasons; the one in order to understand fully the natural processes which surround us and to establish the laws which govern them, the other in order to solve some immediate practical problem. The limits in the first are in the scientist's own hands and are set by the hypothesis he wishes to test or the particular phenomenon he wishes to investigate; the examination of the hypothesis that certain molecular structures are essential for a particular biological activity or study of the processes involved in the control of the wing muscles of an insect in flight will serve as examples of the two different approaches.

In the second the limits are set by the problem put to the scientist; his work in its solution may lead him into the study of natural processes and laws but only so far as they are needed to get the answer he is seeking. It is in the inspiration needed for each type of work that the true difference lies. The applied worker finds his in seeing his work bear fruit in the field; when he has solved one practical problem his desire is to go ahead with the next without tidying up all the loose scientific ends which may remain. The fundamental worker's inspiration lies in his desire for knowledge for its own sake and in that there is a serious potential danger. When such a worker ceases to have original ideas, he goes on collecting facts which either follow existing patterns, such for example as confirming for related species facts or theories already well proved for a number of other species, or still worse the collection of facts without any pattern in the hope that when they are assembled one may emerge by chance. There is much less danger of the applied worker falling into this unprofitable state provided he keeps in close touch with farming practice; he will be stimulated continuously by new and interesting problems. The pit he must avoid is the assumption of omniscience; of providing the glib ready-made answer to every problem.

Although agricultural research covers so many scientific disciplines and calls for both fundamental and applied research workers, there are certain requirements in the undergraduate training common to all those who hope to undertake research in agriculture, or for that matter in any other field.

After patience, the next quality needed for a successful research worker is acute powers of observation; not the type of observation which only sees and remembers, but that which observing two or more apparently separate and unrelated objects or events, grasps that they are related.

The next requirement is for the imagination to see the significance of the relationship and the ability to evolve a theory to explain it.

The theory must then be tested and this involves the ability to design critical experiments and to carry them out with patience, accuracy and the necessary manipulative skill. When the experiments are finished, if the theory is proved wrong, as it will be most often, the research worker must have the determination to go on worrying at the problem, in and out of the laboratory, till he sees the flaw in the old theory and can amend it or work out a new one, and the patience to devise and carry out a new set of experiments.

At last, when he has an acceptable answer to his problem, he must be able to set out his reasoning and his experimental conclusions in a form which others can understand. The complaints of the editors of journals and of the directors of the research institutions suggest that power to do this is becoming increasingly rare.

One other attribute which is of the greatest value to a research worker is a balanced self-criticism. Some men seem to have no critical faculty so far as their own work is concerned, whilst others are morbidly self-critical to a degree which makes it almost impossible to bring any piece of work to conclusion.

These are the qualities wanted in a research worker; to some extent they are inborn, they grow under proper stimulus at school, but it is essentially in the undergraduate and immediate postgraduate years in the university that they can be brought to their full development.

These statements may be platitudinous, they may have been made many times before in one form or another, they amount to no more perhaps than to say that agricultural research requires the same qualities as research in any other field. But that is in fact true and must be said first if we are not to lose sight, in the detailed consideration of the subjects to be studied, of the essential nature of the training needed.

The undergraduate training for agricultural research does not differ from that for any other branch of research in experimental as distinct from descriptive biology. The type of problem to be attacked and the methods used for their solution are the same, it is only the subject-matter which differs.

The facts which are taught to an undergraduate can only be a minute fraction of the basic knowledge in the science he is studying; it is long odds that when he begins his first research problem he will be confronted with the task of acquiring a whole field of new knowledge. In selecting the facts for teaching it is therefore possible to do so with the primary objective of using them for mental training. There are, however, two reservations to this generalization. It is essential that the student should not have all the facts given to him in text-books and lectures, he should have to look up enough himself to obtain at least a nodding acquaintance with a scientific library. The second is that as far as possible the material used for teaching should be such as to arouse the student's interest in the applied branches of his science. Much of the biological material of agricultural interest is stated to be unsuitable for teaching but it is difficult to believe that some could not be selected for the illustration of basic principles.

More important than the factual knowledge is the training given in other disciplines. The modern experimental biologist must be given a training in mathematics, physics and chemistry, such that if his research calls for it he can without undue difficulty become reasonably expert in the use and understanding of the techniques of any one.

It is not sufficient that the young biologist attends a course of lectures in each subject, designed to cover the needs of awide range of students, and goes to practical classes where he carries out a series of experiments he does not fully understand with apparatus laid out ready for him and his text-book propped up on the bench before him. The course of study in each subject should be specially designed for biologists. It should aim at giving a broad understanding of the science, using as illustrations material and techniques which are of importance in the study of the living organism. The practical courses should give the biologist the opportunity to become thoroughly familiar with some of the apparatus and methods which he may require in his later work. It is better that he should do a few experiments well and learn to appraise his results critically, than that he rushes through a long syllabus doing nothing properly and having no confidence in the answers he gets. In chemistry, for example, it is far more valuable for him to do a very limited number of quantitative analyses, repeating them until he can get accurate results, than to try to cover every determination he may need, without ever establishing confidence in his powers as an analyst. One volumetric analysis is very like another and the differences can be found in a text-book. What the student can only learn in the laboratory are the tricks of the trade.

The assessment of the true value of the results of chemical analyses is equally important. The biologist has all too often a touching and entirely unjustifiable faith in the figures which the chemist produces. He should be taught to question the method of sampling, the preparation of the sample for analysis and the biological significance of the results.

This brings us to what is the most important difference between the training of a biologist in the other scientific disciplines and the training of those who are concerned with these disciplines alone. The biologist must never be allowed to forget that his function is to study the living organism which is in a state of continuous change. Many of the methods he must use involve the destruction of the life he is studying. As a result the processes which made up the life of the organism are brought to a stop, and are substituted by another group associated with decay. This second group can be stopped and the material rendered inert by suitable treatment in the laboratory, and it is from the examination of such material that the biologist must draw many of his conclusions. He cannot interpret his data directly as would the chemist or physicist, he must try to assess from the analytical data on the dead material the composition of the living organism before it was killed. If the biologist is to keep his scientific integrity, he must master the principles and techniques of chemistry and physics well enough to be able to weld them into his own science and to direct their use.

In the biochemist and biophysicist we should find this integration, and in many instances we do. In other instances, for example, where the original training has been in chemistry, there is an unfortunate tendency to regard biochemistry as no more than a branch of organic chemistry. The biologist with the necessary training in chemistry is the best safeguard against the extension of this dangerous conception.

The introduction of so much teaching of the related scientific disciplines into the training of a biologist presents a very serious problem to those responsible for the biological teaching itself. It may be asked whether time will be left to cover a reasonable syllabus. It is true that the increased time given to other subjects will force the teachers in biology to select from existing programmes the more essential items and to discard the rest. If, however, the teaching of the other disciplines is specially designed for biologists and the whole course is fully integrated, the position may not be so bad as it at first seems. Many items which now have to be taught as part of the biology course may well find their proper place in the chemistry and physics courses for biologists.

Where a selection has to be made it should be by the exclusion of factual information which is necessary neither for the understanding of the basic principles of the science nor for the training of the student's brain, eyes and hands for research. The student can in his immediate post-graduate training get the particular factual knowledge required for the branch of research he is entering.

This early post-graduate experience is perhaps the most important in a research worker's career. He is applying the principles of his science to a definite problem, testing out the techniques he has learned not as an exercise but in actual practice, acquiring for the first time real confidence in the use of hand and eye and experiencing the misery of failure and the joy of success. It is of the greatest importance that he is wisely guided through this period of development. His problem should be carefully selected to give him the training he needs; he should never be used as an additional pair of hands in the laboratory, working on a small part of some large stock problem. At times it may be necessary to persuade him to leave for a time a problem of his own choosing, because it is so far beyond his powers that he will learn nothing from it.

Very few students can concentrate on a single research problem the whole of their time and energy; moreover, it is good for a man to learn to fit in his research with other work. The postgraduate period should therefore be one in which the student attends more advanced lectures and practical classes in related subjects and for a systematic course of reading not only of text-books and scientific journals but also of the good general literature about the field in which he hopes to work. Agriculture is particularly rich in books which will give the student both an understanding of the timeless underlying problems of the farmer and an appreciation of good prose writing.

Although the acquisition of much of the factual knowledge required by the student can be left to the postgraduate period, the foundations for his later research career must be laid down in his undergraduate years. He must learn to observe, to have imagination, to reason, to plan experiments and to carry them out with patience and manual skill.

Some of these qualities he may acquire by the study of the work of the great original workers in his subject. Too often, in order to include the latest fragment of information which will be out of date to-morrow, the description of classical work of the greatest educational value is omitted because it was out of date yesterday.

But most of the student's training for research must be in the laboratory and the field. Only by long hours spent in the practice of his science will he get the qualities he will need in research. It is not the number of different experiments he does which is important, but the number he does well as the result of his own skill. A man may get the knowledge to pass an examination by looking down a microscope at a number of sections ready cut and mounted with carefully written instructions of what he should look for in each, but he will not in this way be trained as a research worker. For that he must be made to cut and mount sections of different types of material until he can produce a set of good slides in which he can observe and describe unaided the characteristics he is studying. If the student is trained in this more general way he will inevitably only cover part of the syllabus for the present final examination, but the examination is in the hands of the universities and can be changed. The final examination papers of the different university schools call each year for the student to memorize ever more and more factual knowledge; the work reported in the last year's output of scientific papers must be crushed into an already overcrowded course. Slowly and imperceptibly this mass of knowledge is pushing out the time-absorbing training in the principles and practice of our sciences. It is only by comparing a university syllabus of to-day with that of 40 years ago that we see the true extent of the change. It has been stated that roughly one-third to one-half the questions which now appear could not have been asked then because the work on which they are based had not been done, yet little or nothing has been cut out of the syllabuses. The output of research in quantity at least is rising rapidly; it is reasonable to assume that in the next 40 years the sum of knowledge will have grown as much as in the last. Somewhere a halt must be called to this alarming growth in the material which must be packed into lectures or read in text-books and committed to memory by the unfortunate undergraduate. The candidates for postgraduate scholarships are already showing the results of this pressure. Their knowledge is often encyclopaedic, but equally often they seem to have little ability to think for themselves and have not a spark of imagination or enthusiasm. They seem to have been crushed into a dull apathy under the weight of knowledge that has been poured upon them. In scholarship interviews the questions beginning 'Do you know anything about..?' almost invariably open a tap from which gushes information, but questions such as 'What interested you most during your course?' or 'Was there anything unexplained that interested you, so that you felt you would like to try to find the answer?' often bring silence, sometimes a flat uninterested 'No', even on occasion a look of resentment as though this was not playing the game.

Let us keep the undergraduate training general in character and not specialized, but let it be general in the sense that it covers thoroughly the principles and practice of the main discipline and gives an adequate specialized training in those of the related sciences and not in that it attempts to impart more and more factual information about every branch of the science. We have now reached the stage where we expect the student to have to learn in his postgraduate years many of the basic methods and techniques of his science, whilst he is forgetting a large part of the factual material he crammed for his final examination, and without any particular loss because he will probably never want it again, or if he does he will know where to find it. Is it not sensible to reverse this, teaching to the undergraduate the principles, methods and techniques on which the discipline as a whole is based with only such facts as are necessary to do so; leaving the specialized study of a branch of the science with the mass of detail involved to the early postgraduate years?

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THE WORK OF THE NATIONAL AGRICULTURAL ADVISORY SERVICE

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The National Agricultural Advisory Service for England and Wales came into being on 1 October 1946. Its function, in the words of its parent Statute, is to give 'free of charge, technical advice and instruction, whether practical or scientific, on agricultural matters'. The establishment of this national service was a new stage in an evolution that had already occupied 40 years. Development in the period up to 1939 was based on this division between a county service and a provincial specialist service. In these years the universities and agricultural colleges built up a service over most of the country, with specialist staffs covering chemistry, dairy bacteriology, economics, entomology, plant pathology and veterinary science. The local authorities developed, in varying degrees and at varying rates, a system of residential and part-time instruction and of advisory services.

The war years of 1939–45, and the urgent need to expand rapidly home food production, created heavy demands for technical advice. Most of the county education staffs were seconded to the County War Agricultural Executive Committees and, thus, brought officers of the advisory services into a closer relationship with a larger body of farmers and growers than had ever existed before. It was recognized early in the war that when peace returned agriculture would have to play a larger part in our economy than it had done prior to 1939, and this would mean an expansion of scientific and educational services.

So far as agricultural education and advisory services were concerned, a committee was appointed, with The Right Honourable Lord Justice Luxmoore as chairman, to survey the whole field and to make recommendations for post-war development. The Committee reported in 1943 and recommended one advisory service for the whole country. The district, which should not have more than 1000 farms or 100,000 acres, should be the primary unit, in the charge of a district advisory officer with a sound knowledge of basic sciences and farm practice, including farm accounting and farm management. The county should be the next unit, with a county officer in charge to co-ordinate the work of the district officers, and with county specialists. The specialist services should continue to be based on the province and the number of specialists should be increased and embrace a wider range of subjects.

The responsible ministers decided in favour of a national agricultural service with the structure proposed by the Luxmoore Committee but did not accept the proposal which the Committee also made, that education and advice should be managed together by the National Council for Agricultural Education. Instead, they decided that the N.A.A.S. should be part of the Ministry of Agriculture and Fisheries and that agricultural education should continue to be the responsibility of local authorities. The Service started on 1 October 1946, with a strength of just over 1100, which has now risen to about 1500.

The division of labour agreed upon was that the N.A.A.S. would advise the commercial producer while the L.E.A. would be responsible for regular courses of instruction, whether at farm institutes or extra-murally, and also for advice to domestic producers. Experience has shown that there can be no hard and fast line of demarcation and the two Services must co-operate closely and give each other assistance.

The duties of the N.A.A.S. as it has been finally constituted may be summarized as follows:

(*a*) To disseminate, among food producers, scientific and technical knowledge, including particularly such new knowledge as can usefully be applied in the field.

(*b*) To provide advice to individual farmers on technical matters related to food production.

(*c*) To carry out such experiments and investigations as may be required to solve problems and to determine the local applicability of new discoveries and inventions, and to be the means of bringing to the attention of research workers problems that seem to call for fundamental investigation.

(*d*) To provide technical guidance to C.A.E.C.'s who act as the agents of the Minister in promoting food production.

(*e*) To operate, on behalf of the Ministry, various statutory and departmental schemes for the improvement of the standards of agricultural production, the most important being:

  (i) the inspection and licensing of bulls, boars and stallions with the object of preventing the use, for breeding, of inferior animals;

  (ii) the inspection of dairy farms in connexion with the administration of milk regulations;

  (iii) the inspection and accreditation of breeding flocks of poultry;

  (iv) the inspection and certification of growing crops of potatoes, herbage plants and vegetables, from which seed is to be harvested, and of fruit bushes and root stocks which are to be sold for planting; and

  (v) the inspection of crops and plants under plant health regulations.

The N.A.A.S. in its structure has followed the recommendations of the Luxmoore Committee and works on the four levels of district, county, province and headquarters. There is a small headquarters staff in London, and, on the provincial level, the country has been divided into eight provinces, seven in England, and Wales making the eighth. The broad scheme of advisory provinces follows the pre-war pattern, although the number of centres was slightly reduced. The provincial set-up is designed to conform to the agricultural pattern of the country, taking into account the wide variations in climate and soil and in agricultural and horticultural practice, and the diverse nature of the holdings the Service is called upon to serve. The provincial centres themselves were sited as far as possible so as to maintain the close contacts which existed with universities and agricultural colleges.

Each province is in the charge of a Provincial Director, assisted in most cases by a Deputy. The specialist officers are situated at Provincial Headquarters and fall into two groups—the science specialists and the husbandry officers.

Science Specialists

The science specialists follow much the pattern of the old provincial service and include the entomologists, pathologists and bacteriologists, but the chemists have now been split into two groups—the soil chemists dealing with soil and plant nutrition, and the nutrition chemists dealing solely with animal nutrition. They have well-equipped laboratories to assist them in their studies and for carrying out the necessary analytical or investigative work. The functions of the science specialists may be divided into three broad categories: first, to help the officer in the field; secondly, to study the problems of the province by maintaining close contact with conditions on farmers' and growers' holdings; and, thirdly, to form a link with the research workers in research institutes, universities, colleges, so that their findings can be tried out and brought to the attention of the farmers. Furthermore, the science specialist officer not only has to supply answers to the more immediate calls of his colleagues but also, in the longer term interest of the service, has to pursue investigations himself within the limits of his time and capacity. When problems are thrown up which require fuller and more lengthy investigation than the specialist officer is able to undertake it then becomes a matter for the agricultural research service.

Husbandry Officers

As the steady stream of new knowledge has flowed from research and pioneer farmers, it has become evident that in addition to the science specialists an up-to-date advisory service for farmers should also include officers well trained in certain aspects of husbandry, to be a link between research and practice.

The old advisory service contained officers who specialized in poultry and dairying, and in addition there were the livestock officers of the Ministry of Agriculture. With the formation of the N.A.A.S. it was decided to appoint six groups of husbandry officers. In addition to poultry, milk production and livestock, officers were appointed to specialize in crops, grass and machinery. Those Husbandry Officers stand behind the District Officers to support them in their work, help them to solve their more difficult problems; to keep them well informed of new developments in their respective fields, and to arrange the investigation of problems thrown up by farmers. Both the Science Specialists and the Husbandry Officers arrange much of their work through conferences and subcommittees, whereby they meet their colleagues in other provinces and thus are enabled to keep in touch with the whole field of work throughout the country generally and not only in their own provinces.

The County Agricultural Officer

At the county level there is for each county a County Agricultural Officer (C.A.O.). He is the senior N.A.A.S. officer in the county and can be looked upon as the successor to the county agricultural organizer of pre-war days. His duties, however, cover a wider and much more varied field of work than his predecessor's, arising from the extensive developments in agriculture since 1939 and the changes in agricultural administration. He occupies a special position in the N.A.A.S., for he combines advisory and executive functions to a greater extent than any other officer. In addition to being the senior N.A.A.S. officer, he acts also as the chief officer of the C.A.E.C.; is responsible for guiding them in the exercise of their duties and, as head of all the staff employed to service them, must ensure that the work entrusted to them is carried out efficiently. This dual function of the C.A.O. as chief advisory and chief executive officer within the county, and the close integration of the work of the N.A.A.S. in the counties with the C.A.E.C.'s., is a particular feature of the N.A.A.S. set-up. It follows the wartime pattern and, while it must be admitted there are varying views held, all that need be said for the moment is that it works well in practice.

In addition to the C.A.O., the county staff consists of a senior N.A.A.S. assistant, husbandry officers for livestock, milk, poultry, horticulture and machinery, and the District Officers. The development and integration of the whole field is the responsibility of the C.A.O.: much must depend on his inspiration, guidance and leadership. In addition, he is concerned with public relations, for the effectiveness of all the work in the counties rests largely on the goodwill and co-operation of progressive farmers and those who supply their varied needs. He maintains close contact, for example, with the County Branch of the National Farmers' Union and other agricultural bodies such as the National Federation of Young Farmers' Clubs.

The District Officer

The most effective means of giving advice, and incidentally the most satisfying to the advisory officer, is through the visit to the individual farm, where problems can be discussed with the farmer on the spot. The service was organized in such a way, therefore, that the services of the general advisory officer would be reasonably accessible to the farmers he was appointed to serve; he is the first point of contact between the farmer and the Advisory Service. In many cases he is able to deal adequately with the problems encountered; in others he may have to call in assistance from his colleagues at county or provincial headquarters. He works closely with the District Committees of the County Executive Committee, and ideally they, together with the District Officer, should form one team. The District Officer must be able to help and guide them in technical matters and, in turn, he draws on their intimate knowledge of the farming conditions of the district and on their wide experience of practical farming. While the visit to the individual farm still forms the backbone of the District Officer's work, physical limitations of time require that other methods should also be used if the needs of the area are to be served. These include various forms of group approach such as discussion groups; contacts with Young Farmers' Clubs; co-operation with Local Education Authority staffs, local branches of the N.F.U., etc., in arranging farm walks, demonstrations and lectures. All District Officers carry out some experimental or demonstrational work in their areas and also are involved in special surveys or investigations. Examples are: surveys on grassland, fodder beet, fertilizer usage, potato yields, bloat, clover rot, rabbit damage. In fact, where the survey is of a wide nature spread over the country, it inevitably means much of the field work has to be done by the officers in the districts.

Recent years have seen a growing demand not only for technical advice as to the best crop to grow, the best variety of the crop to grow or how to manure it, or how to feed livestock, but for more comprehensive help on the organization of the farm and the economic results likely to arise from making this or that change or following this or that plan. The N.A.A.S. has given a good deal of thought and attention to in-service training to equip its officers with economic data and a knowledge of how to use it, and thus to enable itself not only to meet this demand but in many cases to forestall it and create it. This is perhaps one of the most significant developments of recent years in advisory work.

Horticultural Officers

There is a parallel service of Horticultural Officers at provincial and county levels, and in some intensive horticultural areas there are also horticultural district officers. In addition to carrying out normal advisory work, they are very closely concerned with the various Crop Certification Schemes.

They are also concerned in the various schemes under Destructive Insects and Pests Acts, Sale of Diseased Plants Orders, the Importation of Plants Orders, and the Inspection of Plant Exports, directed to safeguard the maintenance of health among crop plants and to prevent the introduction or spread of pests and diseases. All this work is carried out in conjunction with the Ministry's Plant Pathology Laboratory and has its educational and advisory as well as legal aspects. Much of this will have been described much more fully in previous papers at the Conference by Mr Moore and others.

Experimental work

A description of experimental work undertaken by the N.A.A.S. would require a separate paper, but this brief account of the organization of the N.A.A.S. would be incomplete without some reference, however short, to the volume of this work and the additional facilities which have been provided in recent years.

In order to provide facilities for long-term, intricate, and possibly costly, experiments, it was decided to establish Experimental Husbandry Farms, each representative of an area with a particular combination of soil and climatic conditions. The farms act as out-stations of the research centres and thus provide for the testing of new findings over a number of soil types and under a variety of climatic conditions; and they also provide opportunities to investigate the more important local problems.

Of eighteen farms originally planned, nine have now been acquired and started over the last half a dozen years, and these represent soils that vary from a blow-away sand to an intractable clay, from a heavy silt to a light chalk. Rainfall range is from 22 inches at the farm in Norfolk to over 50 inches on those in Wales and East Lancashire.

The Experimental Farms are neither research stations on the one hand nor demonstration farms on the other. While their primary function is to conduct experiments, it is essential that they should also demonstrate good farming.

Parallel with the Experimental Husbandry Farms, five Experimental Horticulture Stations have been set up. These are situated on different soils and in different climatic regions, their particular sites having been chosen in relation to those of the well-known horticulture research institutions and with regard to the geography of commercial horticultural production. The stations, which work very closely with the research institutes, carry out experimental programmes on fruit, vegetables, glasshouse and intensive crops. In addition, a new station has been acquired in Kent for the National Fruit Trials, and there are three Demonstration Stations for horticulture in Wales.

Experimental work in the Provinces and Counties

The creation of Experimental Farms and Stations does not do away with the need for the continuation of the experimental work carried out on private farms, but rather the reverse. These experiments are planned in each province by a Provincial Experiments Committee, which allows of a co-ordinated and carefully thought out plan of experiments and prevents any unnecessary overlapping or wasted effort. The help and advice of the Statistical Department at Rothamsted Experimental Station is available to these Committees and has been most helpful, particularly on points of design, layout and on the analysis of results. Experiments in this context mean trials where the treatments are replicated so that the results can be analysed statistically and their significance determined. They may be preceded by observation studies consisting of single plots where, although the comparison of yields may be misleading, the appearance of the plots may often suggest a line of inquiry to be followed up in a replicated experiment. The experiment is frequently followed by demonstrations.

The programmes of work at the Experimental Farms and Stations are decided by Committees of the Agricultural Improvement Council, and experimental work in the provinces is also reported to them. In addition to all the many personal and close contacts between members of the N.A.A.S. and the research institutes, official contact is ensured through the Agricultural Improvement Council with the Agricultural Research Council.

WORK OF SOME OF THE SPECIALIST SECTIONS

The broad duties of the Specialist and Husbandry Sections have already been briefly outlined, but it may be of interest if I give a little further detail, of necessity again very briefly, of some sections whose work may most closely concern the interests of this Association. Let me take first the entomologists and pathologists, many of whom are members of this Association and who would, of course, be much more qualified to discuss their work than I am.

Entomologists

The principal duty of these officers is to advise on agricultural and horticultural pest problems. In the words of one of them, they are somewhat akin to the fire service, in that unless prompt action is taken the matter may well become a post-mortem instead of a saved crop.

The identification of pests, how to control them, and the implications for future cropping when chemical control is not possible, are the conundrums which entomologists have to solve daily. Extensive soil sampling for such pests as potato root eelworm and wireworm helps them to give sound advice to farmers on the selection of the best fields to crop in order to harvest the biggest yield and the best sample. Experimental work is an important part of the entomologist's job, and many advances in the use of the old and the newer insecticides have been made by them.

Pest and damage assessment has always been considered of outstanding importance and the scope of this sort of work is decided by the Pest Assessment Committee of the Conference of Advisory Entomologists; and the results are collated by its members. In this connexion, valuable work has been done on the accurate assessment of populations of the mealy cabbage aphis and the damage caused by this pest. More recently, similar work has started on frit fly, an old problem still unsolved. This work has indicated in one year of experimentation how enormous the real loss caused by this pest can be, something which has only been guessed at before. More important still is that a promising lead towards economic field control has been opened up. In some cases the work of the Pest Assessment Committee has led to reasonably accurate forecasting of damage by pests such as the leatherjacket, the bean aphis and mangold fly. This pest assessment work is being followed with interest by other countries.

The potentially important problems are not being neglected either. The flare-up of wheat bulb fly in 1952–3 stimulated an extension in the investigational work already in hand, and many experiments on control were done in 1953–4, as a result of which at least one method of treatment has shown promise. Another example which can be cited is the attention now being directed to the cereal root eelworm—a pest which has been recorded in an increasing number of areas in the past few years. This is a pest which could become serious—perhaps as serious as the potato root eelworm which it resembles in habits but with the added complication of infesting all cereals and some agricultural grasses.

Some provinces, in addition, have special responsibilities because of the incidence of certain pests. For example, the Entomology Department in the South-East Province is concerned with the control of the Colorado beetle. In this work potato fields have to be mapped annually, beetles searched for and precautionary spraying supervised. Some 20,000 to 30,000 acres are dealt with in the South-East Province each year, and it is a tribute to the general efficiency (and the vagaries of our climate) that it is possible to say that Colorado beetle is *not* established in Great Britain. In 1947 over fifty breeding colonies were detected, dropping year by year to two in 1952 and nil in 1953.

Plant Pathologists

The main functions of the Advisory Plant Pathologist are to advise on plant disease problems and to watch the disease pattern in the group of counties which constitute his province. Normally, inquiries from farm or market garden are sent by the District Officer whose aid the farmer has invoked. Experienced field officers are frequently able to assess the position in the field and to take suitable specimens for submission to the specialist. If, after examination in the laboratory, the diagnosis of the disorder is made, then the officer is informed and control measures suggested. Such measures should, of course, be compatible with the practice of the particular holding, and it is here that the liaison with the District Officer is of particular value.

Often, however, the case is not straightforward and the disorder is not simply due to a pathogen attacking a host, or perhaps the normal control measures need modifying to fit unusual circumstances. Where such complexity is suspected or where otherwise appropriate, a joint visit to the holding by the District Officer and the Plant Pathologist may be arranged. It is then that the cultural conditions associated with the crop are carefully analysed to detect the fault.

Items from the actual case book at one of the Provincial Plant Pathology Departments might help to illustrate the work. In this department on 2 June specimens were received for examination from sixteen holdings, as follows: four inquiries related to tomatoes, three to apples, two to wheat, one each to barley, potatoes, hops, blackberry, strawberry, stock and gladiolus. Of these sixteen disorders, pathogens were found to be directly responsible for six, while two cases were passed to the Advisory Soil Chemist for attention. When after laboratory examination no primary pathogen could be found in the remaining eight cases, it was concluded that unsatisfactory environmental conditions were responsible and inquiries into the conditions of growing were started so that errors made this year might be avoided in future. The strawberry plants received proved to be infected by the red core fungus (*Phytophthora fragariae*) and this prompts reference to the plant health work done by the N.A.A.S. The inclusion of administrator, inspector and plant pathologist within the same organization has enabled greater attention to be paid to prevention of disease by suppression at the source. For example, in 1952 the Red Core Disease of Strawberry Plants Order (under Destructive Insects and Pests Acts) prohibited the sale of runners from infected land, and surveys of strawberry-growing districts have been carried out by Horticultural Officers who submitted suspected plants to their Provincial Pathologist for confirmation of the disease. Of at least equal importance to the statutory measures are the voluntary schemes whereby a grower may apply to have certain of his stocks examined in respect of trueness to type and freedom from certain diseases. Crops at present within the Certification Schemes include potatoes, fruit rootstocks, black currants, raspberry canes, strawberry plants and hops. These schemes have proved an undoubted success, and it is clear that growers would welcome an extension of the list if the capacity of the Advisory Service were greater. The Pathologist plays an important part in Certification by assisting the inspector with complex cases and by dealing with problems of disease which are often exposed during inspection visits.

Pathologists from each Provincial Centre co-operate in carrying out a systematic assessment of the loss which a selected disease is causing the country during the year. Such data, collected over a series of years from countrywide surveys, determine its economic importance. A number of diseases, including take-all of wheat (*Ophiobolus graminis*), mildew of cereals (*Erysiphe graminis*), choke of cocksfoot (*Epichloe typhina*), rot of clover (*Sclerotinia trifoliorum*) and mosaic of broccoli (virus) have already received attention. Mr E. C. Large of the Ministry's Plant Pathology Laboratory, Harpenden, is the collator of this work and will doubtless give details of its operation in his talk this afternoon.

Though the commitments in a busy department rarely permit Plant Pathologists of the Advisory Service to undertake long-term research, summary investigations are necessary for the solution of day-to-day problems of local importance. Thus, the value of new fungicides may be tried under conditions peculiar to a district, or pathogenicity tests made to decide whether a virus is responsible for unrecorded symptoms in a plant. Field trials are carried out, and they are often components of larger experiments and are manifestations of the co-operation which exists between the N.A.A.S. and the several national research stations.

Soil Chemists

As knowledge of soils and crop nutrition has developed so has the field of interest of the Soil Chemist. To-day he is interested in a very fascinating field—the many variations in soil conditions that he finds in his area, their origin and influence on soil fertility, the methods by which soil conditions may be improved and the effects of various associations of soil conditions on the nutrition, growth and productivity of a very large number of agricultural and horticultural crops.

Soils are being studied more and more in the field both as media for rooting of crop plants and as suppliers of moisture and nutrients to them. Poor rooting conditions may not only cause stunting of a crop but impair its nutrition even when ample nutrients may be present. The Soil Chemist must have an eye for the healthy plant and for the symptoms which it shows when soil conditions or nutrition are defective.

The problems which come his way are many and varied. Those which have been met many times before fall into the class of routine and present no special difficulties except the provision of adequate space, equipment and staff for dealing with them. More and more problems, however, are being found for which special techniques must be used. Sometimes a crop fails and it is by no means certain as to the cause. If a disease or insect pest does not appear to be responsible the soil is examined for defects in structure, aeration, moisture supply, drainage, acidity or alkalinity and organic matter and those nutrients for which methods of analysis have been established. This may provide the answer but because analytical methods have their limitations it may be necessary to try the response of the crop to a whole range of nutrients. It is well known that crops will take in nutrients rapidly through their leaves, and a technique has been developed of applying up to five mineral nutrients in factorial combination to small plots where crops are failing. The choice of nutrient to be tried will usually depend on the evidence of soil examination and analysis and the symptoms shown by the crop. While the macro elements may sometimes be included it is more usual to try a number of the micro elements. The cause of the complete failure of cereal crops in Woodwalton Fen, Huntingdonshire, was quite unknown until this technique was tried and an outstanding response to copper was obtained. From this result, experimental work developed on the treatment of copper deficiency by foliage sprays and by soil treatment. At present foliage sprays are preferred. Increases in yield from a few hundredweight of grain to over 30 cwt. per acre have been obtained as the result of applying less than 1 lb. of copper sulphate per acre as a foliage spray to cereal crops. As a result of this work the farming of a considerable area of fen peat has been made more flexible and safer, by introducing a profitable cereal crop into the rotation and lessening the risk of root eelworm damage to potatoes and sugar beet. As so often happens, once a trouble has been recognized it is found to be more common than was realized. It is now known that copper deficiency in cereals occurs in many parts of the black fen and on sandy soils which have been reclaimed from heath either recently or a long time ago.

The value of studying soils in the field and understanding their mode of formation and behaviour was well illustrated in the special problem presented when much of the low-lying land along the East Coast and in the river estuaries was flooded by the sea in February 1953. In order to tackle, with limited resources, the extensive soil problems which were created, it was necessary to form a plan of action based on knowledge of the salt contamination of the soil, the drainage conditions and likely rate of removal of salt, the risk of physical damage to the soil resulting from absorption of sodium, the need for gypsum to counteract the sodium, the risk to deterioration of soil structure from cultivations and ploughing, the tolerance of crops to salt and the effects of growing different crops on the restoration or destruction of soil structure.

According to the soil types and conditions found, so were the properties of the soils and their behaviour to salt predicted without any laboratory examination. The main activity of the laboratory was then directed to salt determinations and the need for gypsum as shown by calcium-deficit figures. Cropping and cultivation proposals followed. Salt levels have fallen more rapidly than was expected owing to rainfall above average during the summer months. As it has happened a bolder policy with cropping would have been possible but could not have been foreseen. The physical condition of the soils and the changes produced by suitable and unsuitable cultivations and cropping have turned out as predicted.

Experimental work on the salt tolerance of crops, carried out by the Soil Chemist and the Crop Husbandry Officer, was begun within a few weeks of the flooding and was followed by the establishment on five different sites—in Lincolnshire, Norfolk, East Suffolk, Essex and Kent—of experiments designed to test the long-term effects of different systems of cropping and cultivations on the behaviour and recovery of salt-flooded land.

Crop Husbandry Officers

The work of the Crop Husbandry Officer will vary according to the part of the country in which he is working. In the west and north of the country, for instance, where livestock and grass are predominant, the problems and inquiries which reach him will often be of a different nature from those problems in the traditional arable areas of the east and south. The arable husbandry of the latter regions is absorbing rapidly new scientific developments, and much of the work is concerned with modern techniques such as chemical weed control, fertilizer placement and ware potato storage, to mention but three differing lines of interest.

The readiness with which the new selective weed killers provided by the research worker have been accepted—the growth-regulating substances, the di-nitro herbicides and the many other new chemicals which are in the development stage in the field—has thrown up numerous problems associated with their use. The problems of spray drift, economical and efficient use of spraying machines and the best method of integrating these techniques into traditional husbandry methods are pressing problems with which it is the job of the Crop Husbandry Officer to be familiar, and to give guidance.

Fertilizer placement with cereals is now accepted as a normal husbandry technique, but the benefits to be obtained from the proper placement of fertilizer with row crops such as potatoes, peas and sugar beet is still insufficiently understood by farmers, and many inquiries are received dealing with this subject.

The importance of the potato crop in arable areas is matched only by the high cost of producing the crop. Whilst fertilizer placement techniques can lead to increased crop returns without extra expenditure, there are new techniques of handling the crop for storage which may reduce the cost of production. As an instance of this, bulk storage in buildings and the use of chemicals for inhibiting sprout development can save labour in handling and losses in storage.

Many of these new techniques require to be studied with some care before they can be applied widely on farms and may involve careful field trials. Co-operation is the essence of this work and much of it is done in conjunction with one or other of the research institutes: a further example is the country-wide series of variety trials of principal crops which is carried out by the N.A.A.S. in conjunction with the National Institute of Agricultural Botany.

In conclusion, I would wish to emphasize that, while all the various sections of the N.A.A.S. have their own field of duties, none works in watertight compartments. Each section is dependent to varying degrees on others for the full carrying out of the duties for which the N.A.A.S. is responsible. We are all one team and we hope that we form part of a still larger team comprising the research institutes, the universities and colleges, and the agricultural education services of the Local Education Authorities. The task of all is the common one of working in the interests of the agricultural industry and, thus, to the benefit of the nation.

Crop protection

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SOME BASIC PROBLEMS IN THE APPLICATION OF CHEMISTRY TO CROP PROTECTION*

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In the first volume of the *Annals*, insecticides were reviewed from the chemical standpoint; since that time the subject has extended beyond the confines of chemistry and entomology. The toxicology of insecticides delves deeply into enzymology and electrophysiology. The intrusion of the highly active insecticide, or other chemical used for crop protection, into the environment of the crop plant makes necessary a many-sided attack involving all the biological sciences and has already revealed the paucity of knowledge on the role and properties of the biologically active chemicals already present in that environment and affecting the well-being of the crop plant.

Cooper & Nuttall (1915) wrote: 'We are only just entering upon the scientific study of the preparation and application of insecticides. That our methods have been too empirical in the past is largely due to the lack of co-operation between the economic entomologist and the chemist; neither can hope to achieve real success alone. It is for the entomologist to investigate the various pests, their life history, habits and vulnerability; it is for the chemist to devise and elaborate means of attack, based upon the information supplied by the entomologist and upon the chemical and physical properties of the substances with which he had to deal.'

In the field of crop protection, the co-operation between biologist and chemist, which Cooper & Nuttall found wanting 50 years ago, has long been achieved, and the extent of its fruitfulness far exceeds the estimates possible to those early authors. They could scarcely have foreseen the revolutionary consequences of the discovery of the protective insecticidal activity of certain chlorinated hydrocarbons, nor could they have foretold that within 50 years the elimination of insect-borne disease could become a practical objective. The entomologist's share has developed well beyond the study of the habits and vulnerability of the insect pest, and the attention now being paid to insect physiology and enzymology is but a reflexion of the axiom that 'no insecticide can be used with full efficiency until it is known why and how it kills the insect'. For the same reason, the discovery and practical success of the auxin-like herbicides and plant-growth inhibitors has accelerated progress in studies on the physiology and biochemistry of plant growth. The more recent development of synthetic fungicides such as captan will doubtless lead to a greater attention and interest in the physiology of the parasitic fungi, a subject to which our President has laid a firm foundation and with which Drs Dimond and Horsfall will shortly deal.

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It is apparent from the contents of their paper that Cooper & Nuttall had a true idea of the part that the chemist was to play in the development of insecticides; they had in mind the necessity of a full knowledge of those physical properties which determine the efficient formulation and application of a particular insecticidal compound. Moreover, their conception of the chemistry went beyond the evaluation of stability and compatibility; they foresaw that a systematic examination of the dependence of toxicity on molecular structure would lead to fruitful results. It is by this route that most of the modern biologically active chemicals have been found, and it is well to remember that most of these important discoveries were made within industrial laboratories; examples are the long-term work on the chlorinated hydrocarbons of Lauger, Müller and their associates of Geigy; the 15 years of the inspired and persistent studies on the organo phosphates by Schrader and Kükenthal of Farbenfabriken Bayer. The systematic synthesis and routine testing of large series of organic compounds is work for which the industrial laboratory is well equipped, but the long-headedness and patience of those who sponsored this work is most commendable and a telling rebuff to those in more academic spheres who consider that the industrial view is blinkered by profit and loss accounts. The number and range of compounds found in the past 15 years is adequate evidence of the rich territory of synthetic chemistry still unexplored; every week, indeed, almost every day, produces its patents protecting lengthy lists of biologically active compounds.

From this raw material the applied biologist is encouraged by the manufacturer to select those compounds of promise in some particular control problem. Pressure by the manufacturer, who to survive must have profitable outlets for the products of his research, has in these early days caused emphasis to be placed on exploratory work which generally takes the form of observational field tests.

The second matter which receives immediate attention, for it governs the use of the chemical on edible crops, is the mammalian toxicity of the compound. Although there is much to be deplored in the publicity which has exaggerated the hazards of the new chemicals and has decried their merits, at least two advantages have been gained: the long-term investigation of mammalian toxicity and the search for methods of residue analysis by bioassay and chemical methods. As Dr Holmes will later discuss the contributions of industry to pest control, and as Dr Ripper will describe developments in the problems and methods of application, I can proceed to those other aspects of basic research in crop protection which have come into focus since the publication of Cooper & Nuttall's paper 50 years ago. After a more specific examination of the biochemical aspects of toxicology, I will discuss broadly the consequences which may follow the purposeful intrusion of a highly active biological chemical into the environment of the crop plant.

To be toxic a compound must have at least two properties: the first is the ability to penetrate to and to accumulate at its site of activity within the organism; the second is the ability to interrupt at least one vital process. Penetration and interfacial concentration are dependent on physical properties imposed by molecular configuration. Thought on this subject has been clarified by the brilliant application of thermodynamics incorporated in Ferguson's rule. This hypothesis co-ordinates and unifies the older and more diffuse generalizations such as the Overton–Meyer lipoid hypothesis and Traube's rule, both of which are relevant to narcosis in homologous series, and the Holt boiling-point rule. Moreover, Ferguson's rule provides a theoretical distinction between narcosis and toxicity: in narcosis the activity of the narcotic in the biophase is in equilibrium with that of the external phase; the toxicant enters into a reaction at the biophase which upsets this equilibrium. Yet even with highly active toxicants Ferguson's rule has interesting applications. For example, it provides an explanation of the observations of Langenbuch (1953) on the differential toxicity to Colorado beetle and to flies of lindane applied in different non-volatile solvents, when toxicity is inversely correlated to the ability of the solvent to dissolve lindane. Clearly there must be a break or 'cut-off' in this relationship and this occurs with the solvent in which the insecticide is so insoluble that the solvent acts as a barrier preventing the passage of toxic concentrations of the insecticide. An example of the latter phenomenon is due to Pepper & Hastings (1943), which ascribed the resistance of the fifth instar of the sugar-beet webworm to pyrethrins to the absence of fat in the cuticle. The greater tolerance to DDT of females over male cockroaches was shown by Munson & Gottlieb (1953) to be associated with the greater fat content of the female whereby the thermodynamic activity of the insecticide at the biophase is reduced. An example of an application outside the field of toxicity is from Dethier's (1954) recently published observations on the olfactory responses of the blowfly to the aliphatic aldehydes. The criteria of response he used were the median rejection threshold and the maximum acceptance threshold. When these thresholds were expressed as thermodynamic activities, equal response at equal activity was shown. Dethier concluded that this relationship, which is Ferguson's rule, may be of more general application in olfaction.

The use of thermodynamic activity to equate the biophase concentration with that of the external phase is applicable strictly only when equilibrium is reached. With most of the toxicants which now find use in crop protection this equilibrium is not attained because of the reaction of the toxicant with some component of the organism. Among such reactive components are the sulphydryl groups which for long have been regarded as the site of activity of the heavy metal fungicides, the insecticidal activity of the arsenites and even the bactericidal action of penicillin. The unsatisfactory feature of such hypotheses is the ubiquity of the sulphydryl group in biological systems; the very smallness of the toxic dose seems to necessitate some mechanism whereby a peculiarly vital sulphydryl group is selected for attack by the poison. The success of BAL as an antidote to the sulphydryl poisons suggests that this selective mechanism might be a favoured attack on two sulphydryl groups suitably spaced on the biological interface; the recent discovery of α-lipoic acid and of its biological significance as a growth factor goes far to satisfy the requirements of the sensitive biological component. Lipoic acid, in its reduced form of 6 : 8-dimercapto octanoic acid, possess two sulphydryl groups on carbons separated by a methylene group which could combine with the poison to produce a stable ring system most certain to destroy the ability of lipoic acid to function in pyruvate oxidation and in photosynthesis.

The phosphorylation of chymotrypsin and the cholinesterases is a proved reaction of the organo-phosphorus insecticides and the suggestion that one reason for the toxicity of these compounds as an inhibition of the esterase is supported by the similarity of the signs and symptoms of organophosphate poisoning to those of acetylcholine. However the weakness of the hypothesis is again the absence of evidence of selectivity. TEPP, for example, is so active a phosphorylating agent that it is rapidly hydrolysed by water; about nine-tenths of the cholinesterase of the organism must be inhibited to produce toxic symptoms yet the toxic dose of TEPP is so small that it is difficult to understand how it could be effective unless some mechanism is available by which the cholinesterase is selected for phosphorylation.

The range of speculation open to the chemist in the postulation of possible reactions between toxicant and biophase was severely restricted by the earlier ideas which regarded chemical combination as the formation of electovalent and covalent bonds. Within the past 15 years proof of the existence of weaker bonds such as the hydrogen bond and those produced by the operation of van der Waals's forces and dipoles not only extends the possible reactions but, because these bonds become operative only when the reactive groups fit closely against each other, may account for the extreme specificity so frequently shown in biological reactions. The most recent application of these ideas and of which only a preliminary report has so far appeared, is due to Gunther and his associates (1954) to explain the specificity of insecticidal activity among the DDT analogues. Substitution of the chlorines of DDT by groups of similar van der Waals radii, for example methyl, gives a series of compounds, first synthesized by Woodcock and Skerrett at Long Ashton, which exhibit some DDT-like activity; even the completely methylated compound, ditolyl neopentane, is toxic to mosquito larvae. From this evidence Gunther and his colleagues deduced that the first step in the insecticidal action of DDT is an interlocking of the DDT molecule by van der Waals's forces to the sensitive interface. The Riverside workers presumed that this interface is on the protein of some enzyme which is inhibited by the reaction. A simpler alternative, since no precise evidence that DDT is an anti-enzyme is yet available, is that the permeability of the interface is altered by the adherence of the DDT-like molecule. Because the primary action of DDT is on the nervous mechanism, the interface involved is perhaps the sheath which, according to Hoyle (1953), surrounds the insect nerve; the change in permeability caused by the attachment of DDT is on this hypothesis sufficient to prove toxic.

Within each of these two general theories—that toxicity is the result of enzyme inhibition or of alteration of membrane permeability—the value of the more detailed hypotheses concerning the specific interactions involved is enhanced by the possibility of experimental test. The separation and, in some cases, crystallization of the enzyme system enables *in vitro* work yielding results which can be subjected to the mathematical analysis of enzyme kinetics. Changes in membrane permeability, in so far as they involve ionic mechanisms, can be examined by electrophysiological methods. As a consequence the insect physiologist and biochemist has in the past decade acquired a role in insecticide studies of importance well beyond that envisaged 50 years ago by Cooper & Nuttall.

Yet another field of hypotheses, the significance of which may well transcend all others, is the effect of the toxicant on the nucleoproteins. This topic is all-embracing; it is at the very root of living and is concerned with the machinery of self-duplication, whether of virus or of gene, and with the regulation and orderliness of cell division. If the toxicant disrupts this orderliness it is a carcinogen; if a gene is involved the toxicant becomes a mutagen. The fact that the present range of toxicants includes but a few mutagens is usually attributed to the protection of the nucleus by the cytoplasm and cell membranes. Moreover, in higher animals those cells capable of undergoing meiosis are submerged in somatic tissue. This argument is not attractive to those who are aware of the apparent ability of certain toxicants to accumulate at the sensitive biophase which is often equally well protected. But certainly the large amount of somatic tissue in relation to the genic apparatus in plants and higher animals means a much higher dilution than would be possible in micro-organisms. Moreover, it is with the micro-organisms that many phenomena comparable to mutation have attracted attention. The inconstancy of many fungi in artificial culture has remained the profound puzzle which confronted Prof. Brierley in his Presidential address to the Association in 1934: 'One cannot too clearly realize that an organism never *is* at any moment, it is always *becoming*.' At this stage of our knowledge it is wise to describe this inconstancy by a non-committal term such as dissociation.

To illustrate the phenomenon I will outline the work of Hannay (1953) at the London Science Service Laboratory on the dissociation of *Bacillus cereus*. This group of bacteria includes a number of forms, such as *B. alesti*, *B. thuringiensis* and *B. sotto*, pathogenic to specific insects. Hannay observed, and Steinhaus & Jerrel (1954) have since confirmed, that high pathogenicity to insects is accompanied by the formation of a crystalline inclusion in the sporulating bacterium. The crystalline material is alkali-soluble protein, and Angus (1954) has shown that the protein from *B. sotto* is itself highly toxic to larvae of *Bombyx mori*, the lethal dose by ingestion being of the order of 0·5 μg. per larva. Recently, Hannay has been able to convert *B. thuringiensis* to *B. cereus*; earlier workers have changed both *B. anthracis* and *B. mycoides* to *B. cereus*. Whether or not Hannay will be able, at will, to change one form of *B. cereus* to another, it is too early to say; the point is that these changes are brought about by the purposeful alteration of the culture media in which the bacteria are grown. They are the response of the organism to the chemicals of their environment.

There are other parallel phenomena now known in bacteriology. By treatment with certain chemicals, *E. coli* may be induced to produce the toxic protein colicin, one of a group of bacteriocins, and the ability to produce such toxicants is hereditary. Similarly, in the transformation of *Pneumococcus* to different types, the ability to synthesize a polysaccharide different immunologically is induced by the addition of a deoxyribonucleic acid from a different strain. It may be that all these phenomena stem from the interaction of the chemical and the nucleoproteins. The literature of the subject, and particularly the masterly review of Lwoff (1953), reveals that fascinating stage of development when a single thought might, at any moment, emerge to crystallize present views into a co-ordinated whole and to illuminate at least part of the vast hinterland which separates living and inanimate matter.

These remarkable responses to chemical treatments have great significance when highly potent insecticides, fungicides or weed killers are added to the soil. The consequences of the addition of a potent and persistent insecticide to the environment of the fruit plantation are already familiar; the destruction of beneficial insects by DDT is rightly deplored as an example of the unfortunate results which may follow the indiscriminate use of agricultural chemicals. What then are the likely consequences of the intrusion of an exotic chemical into the complex interplay of the microbial population of the soil? The effective strains of *Rhizobium* are readily dissociated to non-effected or parasitic strains; bacteriophages destroying *Rhizobium* seem to be universally present in soil yet are not always able to destroy their host. These are but two examples of the problems which arise in the use of soil chemicals of high biological activity.

The consequences of the interaction of the pest control chemical and the biological environment of the crop are by no means always detrimental. The practice of soil partial sterilization was originally introduced as a method of crop protection but it is now used more as a method of soil improvement. A recent example is due to Richardson (1954) who showed that the fungicidal activity of thiram added to the soil for the control of damping-off persisted longer than the chemical itself. By killing-off the pathogenic and other susceptible soil organisms, thiram encourages the growth of resistant fungi, to which category belongs *Trichoderma viride*. This fungus is a producer of antibiotics such as viridin and gliotoxin which are known to be toxic to the damping-off fungi and which are the probable cause of the persistence of the fungicidal effects of thiram.

It is still a matter of argument whether the antibiotics produced by so many soil micro-organisms in artificial culture have, under natural conditions, any important influence on ecology. Clearly the main factor operating in the interactions of the biological environment is competition whether for light, air, water or nutrient. Yet evidence such as the example derived from the above-mentioned study of thiram is accumulating to show that antibiotics are important factors in this competition. Indeed, scattered through the literature there are many suggestions and some evidence that competition between higher plants is likewise influenced by toxins. These may arise from the living plant, as in Pickering's classical experiments on the effect of grass on fruit trees, or they may be formed by the breakdown of plant material as is juglone, responsible for the failure of crops grown under walnut trees. There is emerging a new subject, ecological chemistry, concerned with the nature and activity of those naturally produced chemicals which affect plant relationships, whether between plant and plant or plant and animal. The development of this subject is necessary for the foretelling of the probable effect of the agricultural chemical on the ecology and well-being of the crop.

REFERENCES

ANGUS, T. A. (1954). A bacterial toxin paralyzing silkworm larvae. *Nature, Lond.*, **173**, 545.

COOPER, W. F. & NUTTALL, W. H. (1915). Insecticides from a chemical standpoint. *Ann. appl. Biol.* **1**, 273.

DETHIER, V. G. (1954). Olfactory responses of blowflies to aliphatic aldehydes. *J. gen. Physiol.* **37**, 743.

GUNTHER, F. A., BLINN, R. C., CARMAN, G. E. & METCALF, R. L. (1954). Mechanisms of insecticidal action. The structural topography theory and DDT-type compounds. *Arch. Biochem.* **50**, 504.

HANNAY, C. L. (1953). Crystalline inclusions in aerobic spore-forming bacteria. *Nature, Lond.*, **172**, 1004.

HOYLE, G. (1953). Potassium ions and insect nerve muscle. *J. exp. Biol.* **30**, 121.

LANGENBUCH, R. (1953). Über den Einfluss des Lösungsmittels auf die insektizide Wirkung des Lindans. *Z. PflKrankh.* **60**, 167.

LWOFF, A. (1953). Lysogeny. *Bact. Rev.* **17**, 269.

MUNSON, S. C. & GOTTLIEB, M. I. (1953). The difference between male and female American roaches in total lipid content and in susceptibility to DDT. *J. econ. Ent.* **46**, 798.

PEPPER, J. H. & HASTINGS, E. (1943). Age variations in exoskeletal compositions of the sugar beet webworm and their possible effect on membrane permeability. *J. econ. Ent.* **36**, 633.

RICHARDSON, L. T. (1954). The persistence of thiram in soil and its relationship to the microbiological balance and damping-off control. *Canad. J. Bot.* **32**, 335.

STEINHAUS, E. A. & JERREL, E. A. (1954). Further observations on *Bacillus thuringiensis* Berliner and other spore-forming bacteria. *Hilgardia*, **23**, 1.

DIMOND, A. E. & HORSFALL, J. G. (1955). *Ann. appl. Biol.* **42**, 282–287

FIFTY YEARS OF FUNGICIDES

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(With 1 Text-figure)

In the 50 years since the Association of Applied Biologists was formed, there have been major achievements in assuring a stable food supply through the use of fungicides. In 1904 the use of fungicides was in its infancy. In 1954 problems of fungicide development occupy the full time of many plant pathologists in public service and in industry. In the United States alone, sales of organic fungicides amount to millions of dollars annually and the investment in development of new materials is very high. Yet the search for new materials is constantly expanding. This expansion came about only because the use of fungicides is a proven form of crop insurance.

To illustrate how fungicides have achieved their present importance in disease control, two examples of how they have stabilized food production will be presented. Some of the research that underlies these advances will be noted briefly. Perhaps it will then be profitable to sketch a few of the present problems that may represent achievements of the next 50 years. In doing so, one may observe that the achievements of the past have largely dealt with protection of plant surfaces, whereas those of the future are largely concerned with internal treatments and therapy of plant disease.

An outstanding contribution of fungicides to a stable food supply is their use as seed treatments. Although copper sulphate, hot water and formaldehyde were available in 1900, they were messy to apply and often injured seeds. Dry chemicals, coated on seeds, offered greater ease of application and promised freedom from injury. The development of organic mercury compounds and use of copper carbonate had by 1917 yielded two groups of materials on which a start could be made. Continued work resulted in the development of a group of copper and organic mercury fungicides for seeds: copper carbonate, cuprous oxide, Ceresan, Semesan and others. In consequence bunt on wheat, *Helminthosporium* blight on barley, and smut on oats and barley became much less important as diseases. In some cases the incidence of diseased plants dropped from 20% to negligible levels, while yields of grain rose as much as 25% (Large, 1940). The cost of such seed treatment is low and the return on the investment is probably unparalleled in the history of plant protection.

Vegetable seed protection has been similarly rewarding. Treatments of spinach seed costing 30 cents have yielded a $300 gross return. Hundredfold returns are not uncommon. A 67-cent investment in pea seed treatments on a crop planted in wet soil yielded as much as 1000 additional pounds of shelled green peas per acre (McNew, McCallan & Miller, 1951). Both on cereals and vegetables, seed treatments have permitted control of diseases which had formerly been thought uncontrollable. Such fungicides as thiram, cuprous oxide and chloranil now offer protection against damping-off organisms, whereas older treatments were designed only to kill pathogens on the surface of the seed.

Fifty years ago fungicides as foliage protectants offered a new tool in the fight with the fungi; to-day their use is commonplace. The discovery of Bordeaux mixture and the mastery over late blight of potato are exciting stories. Less familiar, perhaps, is the sequel to the late blight story—the development of pesticides for potatoes which in the United States overcame the phytotoxicity of Bordeaux mixture and the inadequacy of older insecticides.

Prior to 1945 the standard spray materials for potatoes in the U.S.A. were Bordeaux mixture and calcium arsenate. In that climate where water is more limiting for plant growth than in Great Britain, sprayed potato vines free of late blight were either dead or in low vigour before the end of the growing season. Horsfall & Harrison (1939) had shown that Bordeaux mixture increased cuticular transpiration and the phytotoxicity from Bordeaux mixture on potatoes was shown to reduce potato yields separately from insect damage by Horsfall & Turner (1943). McCallan (1946) ranked the combination of Bordeaux mixture injury and insect damage as the most serious among potato disorders in the U.S.A. From 1942 to 1945 the ethylene bisdithiocarbamates, nabam and zineb, were being developed and coming into use by potato growers along with DDT. This combination eliminated the injurious effects of spray and insects. By 1950 the combination was almost the standard potato spray in the U.S.A. From 1939 to 1952, the yield of potatoes per acre doubled in the U.S.A., the increase occurring from 1945 onwards (Fig. 1). The contribution of these materials to increased yields through eliminating phytotoxicity and effecting high levels of disease and insect control has been shown many times (Table 1).

Significantly, the average potato yields in Great Britain from 1939 to 1952 were always higher than the averages for the U.S.A. and did not change very much within this period except in two years when yields dropped severely. The constantly higher yields in Great Britain, despite continued use of Bordeaux mixture and other copper sprays, suggest that phytotoxicity and insect injury, even if they did increase transpirational losses, did not affect the plant critically because of the wetter climate. If so, the phytotoxicity of Bordeaux mixture in Great Britain is of small consequence to the plant and organic fungicides would be expected to offer fewer advantages in this climate than in the U.S.A.

Recent studies on the nature of fungicidal distribution and redistribution suggest that this reasoning is correct. The organic fungicides as a group have a lower tenacity than has Bordeaux mixture. Moreover, analyses of deposits on leaves sprayed with copper fungicides have shown them to be redistributed on the plant and thus to protect surfaces not covered initially. Experience with the DDT-nabam or zineb spray combinations have shown that potatoes must be sprayed more frequently and coverage must be more thorough than when Bordeaux mixture is used for blight control. Rich (1954) has recently compared Bordeaux mixture and zineb with respect to build-up of deposit and its redistribution or deterioration in weathering, and has suggested a basis for predicting when redistribution will occur.

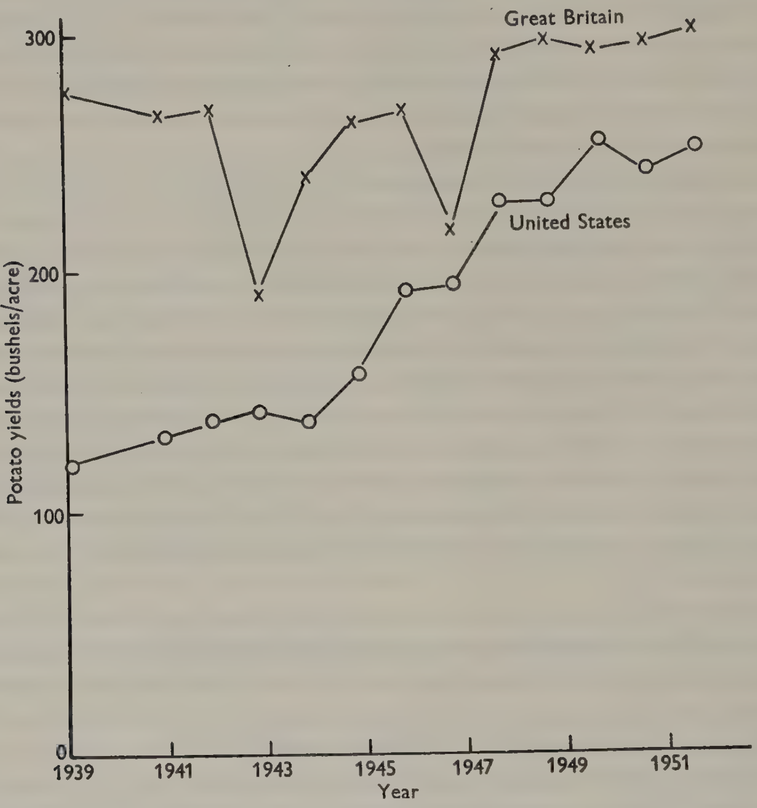

Fig. 1. Yields of potatoes in Great Britain and the U.S.A. for the period 1939 to 1952. Source of data: Agricultural Statistics, United States Department of Agriculture.

TABLE 1. *Effect of fungicides and DDT on yield of potatoes**

Fungicide	Yield (bushels per acre) No DDT	DDT
Check	236	398
Bordeaux mixture	311	507
Nabam, $ZnSO_4$, lime	333	618

* Data of Berkeley, Thompson & Richardson (1946).

These two fungicides deposit in a strikingly different manner, Bordeaux deposits behaving as though adsorbed to the leaf surface, whereas zineb deposits behave as though they were not. Bordeaux particles in water bear a positive and zineb particles a negative charge, whereas the electrokinetic charge on the wet leaf surface is negative. The charges on leaf surface and fungicide therefore favour adsorption of Bordeaux mixture but not of zineb. Such deposits assume a charge again when wet by rain and Bordeaux residues behave as though held by the leaf. What is freed is picked up again through adsorption by the unprotected leaf surface. Zineb does not behave in this way. Consequently, the zineb deposit diminishes rapidly and does not become redistributed. Attention to the role of electrokinetic charge on fungicides in adsorption to the leaf surface may permit the development of materials having greater fungitoxicity than Bordeaux mixture but retaining its tenacity and ability to redistribute on the plant. These factors are of importance in direct proportion to the frequency of rainfall in the climate in which the fungicides are to be used. One would predict that present organic fungicides would perform better in regions of moderate rainfall than in regions of frequent rainfall. Then organic fungicides would find a place in disease control in areas of high rainfall only when, because of their high specificity for a given pathogen, they offered a unique advantage as ferbam does for control of the rust diseases and as ferbam and zineb do for control of downy mildew of tobacco.

The practical achievements in control of disease by fungicides have depended in the main on laboratory assay methods for measuring fungitoxicity and tenacity. Only through these assays could modern fungicides be developed on the scale they are to-day. The emphasis has gradually turned to studies of the relation of structure to toxicity of molecules (Horsfall & Rich, 1951). This shift in emphasis has led to the concept that a fungicide improves in toxicity as it is enabled to enter the cell more readily, and that in a number of organic fungicides, one can distinguish the toxophore (the fungitoxic moiety) from the lipophore (the fat solubilizing groups) (Rich & Horsfall, 1952). Studies on the ultimate fungitoxicant of such materials as nabam have suggested a chain of chemical events which may precede killing of the fungus spore (Rich & Horsfall, 1950; Ludwig, Thorn & Miller, 1954, Klopping & van der Kerk, 1951).

Perhaps the outstanding problem for the future involving protective fungicides is the high likelihood that strains of fungi will arise which are resistant to materials now effective, a problem already serious in economic entomology and in medicine. It may be that in practice too small a proportion of the inoculum in a given site is exposed to a fungicide at one time to increase appreciably the odds for development of resistance. Would it not be worth while now to examine whether or not this is so? The present high cost of developing new fungicides and inevitability of having to process a logarithmically increasing number of test compounds for each new fungicide that reaches the market pose serious problems in this connexion. If resistant fungi are likely to develop, we should take steps now to diminish that possibility. Three courses are open to us, some more feasible than others. One may (1) search for fungicides which have multiple toxic mechanisms against each pathogen for which they are used, (2) use two fungicides, each having different toxic mechanisms and always apply them in combination, or (3) apply fungicides to resistant varieties of the host. If these suggestions sound extreme, recall how it would have sounded in 1944 to suggest that DDT would not always be adequate to combat houseflies.

When one problem in food production is solved, another arises in its place. The control of potato blight by Bordeaux mixture created another problem—phytotoxicity on the potato plant—which was of consequence in reducing potato yields. Correction of this problem through development of non-phytotoxic fungicides has resulted in potato vines which remain lush to the end of the growing season. Now growers can see the extent to which *Verticillium* or *Fusarium* wilts reduce the vigour of the plant during the last half of the growing season, the time when vines must be vigorous to produce large tubers. Verticillium wilt of potatoes has assumed importance in the U.S.A. since 1945, not because it is a new disease but because the damage it causes can now be seen.

For wilt diseases, whether of bacterial or fungal origin, protective fungicides are ineffective. Within the past 10 years, considerable progress has been made in learning to control these diseases which enter the host through insect feeding wounds, through roots and natural plant openings. Both the antibiotics and synthetic plant chemotherapeutants are proving useful in controlling plant diseases within the host. The use of antibiotics in plant disease control has recently been reviewed by Brian (1954), who, with his colleagues, has pioneered in these studies. Control of fire blight of apple and pear (Kirby, 1954; Goodman & Hemphill, 1954) and of the bacterial diseases of vegetables appears assured in the next few years. Likewise the development of compounds which permeate the host and make it resistant to disease or which kill the pathogen offers promise for plant disease control in the future (Crowdy & Wain, 1951; Dimond, Davis, Chapman & Stoddard, 1952). This technique is already in use by commercial growers in Connecticut for control of *Fusarium* wilt of carnations (Stoddard & Dimond, 1951) and of red stele on strawberry (Stoddard, 1951). Also there is hope that the cereal rusts will succumb to chemotherapy. A year ago calcium sulphamate was reported to reduce materially the incidence of leaf and stem rusts of wheat materially when applied as a spray concentrate from aircraft (Livingston, 1953). We may hope that the 100th anniversary meeting of the Association of Applied Biologists will see these approaches to disease control reduced to commonplace practice.

REFERENCES

Berkeley, G. H., Thompson, R. W. & Richardson, J. K. (1946). Potato spray tests in Ontario. *Amer. Potato J.* **23**, 285–91.

Brian, P. W. (1954). The use of antibiotics for control of plant diseases caused by bacteria and fungi. *J. appl. Bact.* **17**, 142–51.

Crowdy, S. H. & Wain, R. L. (1951). Studies on the systemic fungicides. I. Fungicidal properties of the aryloxyalkyl carboxylic acids. *Ann. appl. Biol.* **38**, 318–33.

Dimond, A. E., Davis, D., Chapman, R. A. & Stoddard, E. M. (1952). Plant chemotherapy as evaluated by the *Fusarium* wilt assay on tomato. *Bull. Conn. agric. Exp. Sta.* no. 557.

Goodman, R. N. & Hemphill, D. D. (1954). The effects of indole-3-acetic acid on the plant disease inhibiting properties of antibiotics. *Science*, **119**, 347–8.

Horsfall, J. G. & Harrison, A. E. (1939). Effect of Bordeaux mixture and its various elements on transpiration. *J. agric. Res.* **58**, 423–43.

Horsfall, J. G. & Rich, S. (1951). Fungitoxicity of heterocyclic nitrogen compounds. *Contr. Boyce Thompson Inst.* **16**, 313–47.

Horsfall, J. G. & Turner, N. (1943). Injuriousness of Bordeaux mixture. *Amer. Potato J.* **20**, 308–20.

Kirby, R. S. (1954). Effectiveness of antibiotics for apple fire blight control under epidemic conditions in Pennsylvania. *Plant Dis. Reptr*, **38**, 432–3.

Klopping, H. L. & van der Kerk, G. J. M. (1951). Organic fungicides. V. Chemical constitution and fungistatic activity of aliphatic bisdithiocarbamates and isothiocyanates. *Rec. trav. chim.* **70**, 949–61.

Large, E. C. (1940). *Advance of the fungi.* New York: Henry Holt and Co.

Livingston, J. E. (1953). The control of leaf and stem rust of wheat with chemotherapeutants. *Phytopathology*, **43**, 496–9.

Ludwig, R. A., Thorn, G. D. & Miller, D. M. (1954). Studies on the mechanisms of fungicidal action of disodium ethylene bisdithiocarbamate. *Canad. J. Bot.* **32**, 48–54.

McCallan, S. E. A. (1946). Outstanding diseases of agricultural crops and uses of fungicides in the United States. *Contr. Boyce Thompson Inst.* **14**, 105–16.

McNew, G. L., McCallan, S. E. A. & Miller, P. R. (1951). Treatments for vegetable seeds. *Canning Tr.*, **73**, 6–8, 21–3.

Rich, S. (1954). Dynamics of deposition and tenacity of fungicides. *Phytopathology*, **44**, 203–12.

Rich, S. & Horsfall, J. G. (1950). Gaseous toxicants from organic sulphur compounds. *Amer. J. Bot.* **37**, 643–50.

Rich, S. & Horsfall, J. G. (1952). The relation between fungitoxicity, permeation and lipid solubility. *Phytopathology*, **42**, 457–60.

Stoddard, E. M. (1951). Control of strawberry red stele by chemotherapy. *Phytopathology*, **41**, 858.

Stoddard, E. M. & Dimond, A. E. (1951). The chemotherapeutic control of Fusarium wilt of carnations. *Phytopathology*, **41**, 337–40.

Ripper, W. E. (1955). *Ann. appl. Biol.* **42**, 288–324

APPLICATION METHODS FOR CROP PROTECTION CHEMICALS

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(With Plates 7 and 8, and 2 Text-figures)

'No chemical is better than its application.'

I. Introduction

The last half-century has seen great developments in the application methods of crop protection chemicals; these were judged so successful by the agriculturists that many became accepted practice and are profitably used on a grand scale in nearly all parts of the globe where men live by cultivating plants. More than 100 million acres have been so treated the world over in the past year.

The application method of a crop protection chemical has decisive influence on the effect of the phytopharmaceutical on the noxious organism to be controlled, also on the crop plant present, and on the population density of beneficial and injurious forms of life in the habitat.

The interdependence of phytopharmaceutical and application method, once recognized, was a powerful stimulus to further developments on either side. A survey of the present status of application methods is difficult because of the complexity of the subject. We must assume a knowledge of A. W. A. Brown's book *Insect Control by Chemicals* (1951), Kearns's work on fruit sprayers (1945), Potts & Garman (1950) and Potts, Garman, Friend & Spencer (1950) on mist blowers, and Akesson & Harvey's paper on chemical weed control (1948), and endeavour to bring their story up to date, to classify the application equipment which has become established and cite the underlying principles as far as they are understood to-day.

The application of crop protection chemicals can be effected in five ways, namely:

(1) application directly to or injection into the plant

(2) release into the air with diffusion to the target (crop and tree fumigation)

(3) release or propulsion through the air to the target either (*a*) in the solid, or (*b*) in the liquid state

(4) injection into the soil

(5) release into irrigation water.

II. Application to and injection into the plant

One of the earliest methods of crop protection was the application of insecticides to growing plants and the brushing of mechanical barriers, insecticidal and fungicidal substances on to the bark. The immersion of plants during transplanting into insecticidal, acaricidal, fungicidal or nematicidal washes is also older than this Association and is still much practised. Individual plants or trays or baskets full of plants are lowered into a tank containing a slurry or solution of the phytopharmaceutical and the plants are thereafter either directly transplanted or dried before transplanting.

Recent applications of treating the aerial organs of the plant are: Nicol (1950), in West Africa, has applied DDT emulsions by means of a brush to small cocoa trees using small quantities of insecticide under conditions where spraying is impossible, and has succeeded in protecting the trees against cocoa capsids. Bond, in Kenya (1953), has shown that the coffee mealybug can be killed by the application of the systemic insecticide dimefox directly on to the bark of the coffee tree by a method of banding; Jeppson, Jesser & Complin, in California (1952), had similar success on citrus trees with schradan and demeton.

The brushing of growth-regulating weedkillers on to foliage of weeds growing in close proximity to cultivated plants is used where a selective weed control effect is desired, despite the susceptibility of the cultivated plant to the same weedkiller, for instance MCPA is brushed on to bindweed leaves climbing on ornamentals.

The direct application method is also used for disinfection, disinfestation and treatment of seeds, tubers and bulbs. Germicidal seed treatments are widely used against many seed-borne diseases, and are of great economic importance. Seed dressing equipment consists of containers for the phytopharmaceutical and dosage equipment, a revolving container, either mounted on an eccentric axle with or without baffles or a stationary horizontal or inclined mixing hopper in which seed and germicidal powder get thoroughly mixed. The adjustable germicidal powder supply is regulated by a metering chain or a rotary valve so that the powder is applied in proportion to the weight of grain passing through the seed dresser; modern equipment also has provision for knock-out devices stopping the grain feed if the supply of phytopharmaceutical is interrupted.

In order to prevent the dust hazards which may arise during the use of germicidal powders or through handling of treated seed, liquid treatments are attempted in some modern installations whereby a germicidal slurry or solution is atomized into the mixing chamber. While this method clearly minimizes the dust hazard at the time of operation, there is little evidence that cereals treated with liquid germicides when dried and bulk handled may not constitute a poisonous dust hazard. Seed treatment is not only used for fungicides but also for insecticides and combinations of the two. For tubers and bulbs the method is modified and provides for immersion tanks with a slurry of the phytopharmaceutical through which the bulbs or tubers are taken on a conveyor and then are allowed to drain, are dried and finally bagged.

The *injection of plants* is also an old technique, and injection of arboricide into trees is well established and widely practised, particularly in Malaya where sodium arsenite is used to kill unproductive rubber trees.

A refined method has been worked out for systemic insecticides by Hanna, Heatherington, Houlton, Edson and the writer, which is called *trunk implantation.* A hole is bored at an angle of 45° to the main axis of the tree under antiseptic conditions, the hole is cleared from 'borings' by air blast, an aluminium plug with a coarse thread is inserted, which grips the wall of the bore hole close to the orifice, thus leaving a chamber for the insecticide between the plug and the bottom of the hole. The plug has a central hole through which the insecticide is applied through a modified veterinary syringe equipped with a long stainless steel needle; thereafter the wound is closed antiseptically. Callus forms around the plug but the centre hole can be re-opened for re-treatments without interfering with the callus formed.

While this method is still somewhat laborious, there are obvious possibilities for its mechanization. Hanna & Nicol (1954) demonstrated great savings in the quantity of systemic insecticide necessary to get a good control of the cocoa mealybug as compared with the uptake of the same chemical from the soil. The other advantage of this method, which it shares with bark and soil application, is its selectivity, as only sucking insects can reach the toxicant; hence pollinators, parasites and predators are not affected (Ripper, 1951).

III. CROP AND TREE FUMIGATION

While many crop protection chemicals applied as dust and spray have a short-range effect as fumigants, the release of a fumigant into the air and the reliance on diffusion of the phytopharmaceutical to reach its target has seen little progress in the last decade; the method is going out of use because of the difficulty in handling fumigation tents over trees and gas-proof dragsheets for ground crops and their wear and tear. Fumigation is still used to some extent in citrus culture but it is laborious and expensive, and some insect species have become resistant to the most popular fumigant, HCN. Crop fumigation with nicotine vapours, while effective and very selective against aphids, has been rendered obsolete by the introduction of systemic insecticides such as schradan which are equally selective but much simpler to apply.

IV. RELEASE OR PROPULSION ON TO THE TARGET THROUGH THE AIR IN THE SOLID STATE

Crop protection chemicals in the solid state are used as a dust or in granular or pelleted form. Twenty years ago dusts were the most widely used methods of chemical control but they have since become somewhat obsolescent because of a number of disadvantages.

Phytopharmaceutical *dusts* when emitted through a blower consist of a mixture of discrete particles, some of which are agglomerations which may consist of as many as 25 to 300 particles. Such agglomeration induces wide variations of settling characteristics even in otherwise uniformly fine ground preparations (Brown, 1951).

The shape and specific gravity of dust particles have a decisive influence upon settling characteristics; a uniform distribution of the active ingredients on the plants is essential, but few formulations of insecticides, fungicides and weedkillers in dust form stand up to a fractionation by winnowing, and active ingredients and diluents fall out in separate parts of the trajectory of the dust. Every biological specification for a dust should stipulate that the active ingredient cannot be separated from the diluent in such a way. There are two ways of ensuring this: (*a*) the selection of a diluent of exactly the same specific gravity and particle shape as the active ingredient; (*b*) by coating the individual diluent particle with a shell of the active ingredient which is deposited on every particle.

Apart from this difficulty, which does not arise with a homogeneous chemical such as sulphur dust, experiments have shown that the unit catch of active ingredient in dust form is smaller than in spray application, as was demonstrated by Laakso & Johnson (1949). This lower dynamic catch by the plant produces lower efficiency of the dust as compared with the same quantity applied as a spray.

Clouds of toxic or phytocidal dusts constitute an important drift problem, and the hazard of toxic materials drifting out of the treated area is more serious than the decrease in deposits within the area; efforts to increase the deposition by the addition of oils or water to dust before emission, which may well lead to an agglomeration of the particles while in flight, have not always increased the degree of deposition on the target, but they do increase the adherence of the dust once it is deposited. Because of this drift problem, dusting of hazardous material is only safe under conditions of near calm, namely up to a wind speed of 3 m.p.h., which, in climates like ours, very considerably restricts the hours in which this application method can be used. These difficulties and the greater cost of any solid diluent over water under most conditions, has made dusting obsolete in all applications but those where the active ingredient is applied undiluted, for instance in sulphur dusts.

Notwithstanding this, interesting advances have been made in *dusting machinery* which until recently suffered severely from the disadvantage that the dosage varied as the dust load in the hopper decreased at the same setting of the discharge regulator. Well-agitated dusts behave somewhat like a fluid and the head of dust in the hopper has a great influence on the amount discharged through the orifice at the bottom of the hopper. The first proposal to overcome this deficiency provided for an elevating helix which metered the dust from the hopper to the intake of the fan. A very elegant solution was found by Schütz (1949) who uses a rotating hopper and scoops up the same quantity of material with every rotation and feeds that to the inlet of the fan. Lane (1954) has developed for an experimental duster a hopper in which a moving conveyor forms the floor of the hopper, and the discharge into the fan is controlled by a gate with a vertical adjustable shutter to regulate the thickness of the dust layer which leaves the hopper on the conveyer belt independently of the 'head' of dust in the hopper.

Both devices have merit but whether they will, in conjunction with coated dusts and other improvements in the formulations to prevent winnowing out of the active ingredient, bring about a renaissance of dusting remains to be seen. A team at the National Institute of Agricultural Engineering is concerned with a study of the influence of electric charges on dust deposition (Cashmore, 1954). Muir's hypothesis that charged particles may produce better deposition requires further investigation, and some workers claim that a charge may produce uneven deposits; charged particles may stand out on the insect integument like iron filings on a magnet, as Wilson & Janes (1942) have demonstrated, thus not helping the diffusion of the active ingredient into the insect body.

On the other hand, the application of solids in the form of *granular* or *pelleted phytopharmaceuticals* has proved a valuable addition to application techniques. Granular insecticides are a formulation of an active ingredient with filler and glue, and are applied by fertilizer drills, fertilizer distributors on aircraft, or even by hand. Granular insecticides and weedkillers are applied either alone or mixed with fertilizers. The advantage of granular insecticides and weedkillers is that they can be very accurately placed on to the target as their free-fall assumes considerable velocity and they are not much affected by wind or drift. Another advantage of granular and pelleted phytopharmaceuticals is that they enable the application to reach the target soil or target water surface even when this is obstructed by vegetation. For the control of banana thrips in the West Indies granular dieldrin in pellet form containing 25 % of the active ingredient is successfully applied by aircraft; the granular insecticide bounces off the banana foliage and reaches the ground where it kills thrips without loss on the foliage. Another good example, although not falling within the scope of this paper, is the treatment of water against mosquitoes despite dense vegetation. Giess (1953), in Southern Pennsylvania, found that almost 100 % of insecticides such as Rothane, DDT and DDD found their target, namely water surface, through practically any kind of tall vegetation, consisting of reeds, tall grass and rushes, which had made the use of liquid larvacides impossible.

There are obviously many possibilities for this application method in temperate and tropical climates against pests that have hitherto been difficult to deal with by liquid sprays and dusts. In this country this method will help further in some cases to prevent the death of wild life and game because by treating the soil, contamination of the vegetation and the adherent moisture, on which the game feed and drink, is avoided.

As Whitehead (1953) has pointed out, the application of granular or pelleted phytopharmaceuticals can be carried out successfully during periods of greater air movement than dusting and spraying; the aerial application can therefore be extended through more hours of the day and is thus more likely to make air application more economic and certain. An obvious application in Britain and many other countries is the treatment of grassland, lowland, marshes and marginal land by weedkillers or weedkiller-fertilizer mixtures.

V. RELEASE OR PROPULSION ON TO THE TARGET THROUGH THE AIR IN THE LIQUID STATE

When phytopharmaceuticals are used as liquids or suspensions and are propelled through or released into the air on to the target in a dispersed form, very different degrees of dispersion are required for various tasks of crop protection; a selection of the most effective degree of dispersion often makes the difference between success and failure and always has an influence on the economy of the crop protection operation.

Physics of the spray process

In order to understand the performance of sprays a knowledge of certain physical phenomena connected with the disintegration of liquids into droplets is essential. Physicists and engineers have investigated the atomizing process, and our knowledge is based on work by Sauter (1926), Scheubel (1927), Rosin & Rammler (1933), Castleman (1931), Nukiyama & Tanasawa (1938–40), Lewis, Edwards, Goglia, Rice & Smith (1947), Taylor (1948, 1950), Lane (1951), Green (1950) of the Chemical Defence Experimental Establishment at Porton, and in particular by Fraser & Eisenklam (1953) at the Jet Research Laboratory of the Department of Chemical Engineering, Imperial College, who with the support of the Agricultural Research Council have greatly contributed to a more precise knowledge of the spray processes.

A common type of *hydraulic atomizer* is the whirl chamber nozzle; the liquid rotates in a whirl chamber and issues from the nozzle orifice in the form of a hollow cone. In the fan spray nozzle—widely used in weed control and in common use as industrial gas burners—the liquid is forced into two opposing jets inside the nozzle tip with the result that a fan-shaped sheet of liquid issues from the nozzle orifice.

Centrifugal atomizers such as the rotating disks used on certain fine-spray generators (Walton & Prewett, 1949), and recently on aircraft sprayers, consist of a rotating disk or cup fed centrally upon the surface with the spray liquid. A thin sheet of liquid is formed on the disk and breaks up into droplets on the rim of the disk (Fraser & Eisenklam, 1953).

With *twin fluid atomizers* such as airblast nozzles, air is introduced under pressure and shatters the liquid. The atomization is effected by tearing ligaments of liquid from the stream of liquid. The ligaments eventually break into drops. Films of liquid, which are stretched, burst and contribute to the drop formation in addition to the ligaments. The resulting drops can be very fine.

The principle of disintegration of a liquid into drops is an increase of the surface area of the sheet or rod of liquid until it becomes unstable and breaks up into droplets. The turbulent flow conditions in the nozzle orifice and the air resistance to liquid issuing from the nozzle at a high spray velocity make for instability of the sheet of liquid.

The development of the liquid sheet was found by Fraser & Eisenklam (1953) to be much influenced by the spraying pressure, the viscosity and surface tension of the spray liquid and conditions of the ambient air. With liquids of a density around 1·0 an increase in the viscosity lengthens the sheet and an increase in surface tension contracts it but makes it more placid.

Fraser & Eisenklam (1935) describe three types of disintegration of the sheet of spray liquid:

Rim disintegration. Surface tension causes the liquid rims of the sheet continually to contract and threads are pulled out from the straight rims during contraction; these and the rims themselves produce larger drops than are formed from the free edge of the sheet.

Perforated sheet disintegration. Disturbances cause the sheet to disintegrate into a lacework of threads of spray liquid. The holes in the lacework expand, holes coalesce and threads of liquid so formed disintegrate.

Wavy sheet disintegration. The surrounding atmosphere causes wave disturbances in the thin liquid sheet issuing from the spray nozzle and these waves tear away pieces of the sheet.

The perforation of the sheet prior to disintegration is, according to Fraser & Eisenklam (1953), caused by the turbulence in the nozzle and by the presence of non-wettable particles.

To produce a good spray it is important to have reasonably uniform droplets. The disintegration of liquid sheet so far described leads to disorderly break-up which results in a very *wide* drop spectrum. An *orderly disintegration* by controlling an orderly formation of holes in the sheet has so far proved unsuccessful, but it was found that with a spinning disk the region of disintegration can be controlled below a maximum critical flow rate. The sheet thins out along the disk until its thickness at the rim is suitable for immediate drop formation; each drop carries two satellites which together form only 15% of the total volume sprayed and hence narrow bands of drop size spectra result, well separated in space from main drops and satellites.

In order to characterize the disintegration obtained by a certain atomizer nozzle under given conditions, a characteristic figure is necessary. Such a central figure must reflect the state of dispersion of the mass of the spray and the presence or absence of the larger droplets, which have over-riding importance because they contain the major quantity of the dispersed spray liquid.

For this purpose the median diameter by mass, generally described as *mass median diameter* (M.M.D.) is often used. This is the figure which 'divides the total volume of the spray into two equal parts; one half of the mass of the spray is contained in droplets of smaller diameter than the M.M.D., and the other half is contained in droplets of larger diameter' (Brown, 1951). The value of M.M.D. is determined by computing the volume in each size class of spray droplets and plotting the cumulative figures of each droplet size class expressed as percentages of the total droplets in the spray against the droplet sizes.* The intersection of the straight line connecting these plots with a horizontal line going through 50% gives the mass median diameter.

For this purpose the diameters of droplets collected on paper are measured and counted after making allowance for the spread factor. This method is widely used, being straightforward but tedious. To mechanize the procedure, Gucker & O'Konski (1949) have used a photoelectric cell in conjunction with a scaler counter for counting small droplets. Recently, Hoare (1954) at the National Institute of Agricultural Engineering counted and sized droplets by a light stream in a similar manner to a television screen. As the light passes over the spots, it reflects lower intensities of light which are magnified electronically and which are counted into size groups automatically. At the Conversazione of this Jubilee Conference a further improvement of this apparatus was exhibited by which Hoare hopes to be able to screen directly from an oscillating platform so that his method should now be able to size and grade down to a diameter of 20μ.

Apart from the M.M.D., one other central figure to characterize a spray as to its droplet size has been proposed: the *Sauter mean diameter*, written SMD or D_0 by the Japanese investigators, Nukiyama & Tanasawa (1938–40) who produced a formula for the atomization of liquid. The Sauter mean diameter is the diameter in microns of a single droplet with the same ratio of surface to volume as the entire spray.

It is claimed that the use of this figure to characterize the dispersion is superior because of the sensitiveness of the M.M.D. to the presence of a few larger sized droplets in the sample counted.

The value D_0 is smaller than the mass median diameter, being between one-half and three-quarters of it, depending on droplet size distribution. Lewis *et al.* (1947) have shown how to relate the value of D_0 and M.M.D.

The fate of spray droplets

A study of the fate of small droplets approaching a twig or branch gives information on which to base specifications for droplet sizes depending whether the crop protection task requires maximum deposition or, on the contrary, long flotation in air, as in the case of space sprays.

Brooks (1947) has demonstrated that an air stream approaching a twig or the side of a cylinder has the frontage of air matching the cylinder diameter split into two streams which pass on either side in such a way that the sum of the cross-section of these air streams is only 75% of the original frontage; as the stream lines on either side of the cylinder get closer, so is the speed increased. Droplets which approach the cylinder in the exact centre of the air stream fail to clear the obstruction, but this filtering effect by the obstruction involves only a small proportion of the droplets that impinge. Most of the small droplets approaching on either side of the impingement area have insufficient kinetic energy to penetrate the boundary layers and follow the stream lines around the obstruction and miss. Larger droplets which have sufficient inertia to resist the angular change in the direction of the stream lines are not sufficiently diverted from their course and therefore impinge on the cylinder and are deposited by impact precipitation. Equally small droplets travelling at much higher speed, as for instance spray mist from a spray blower, have sufficient kinetic energy to resist the change in direction, penetrate the boundary layer and are deposited.

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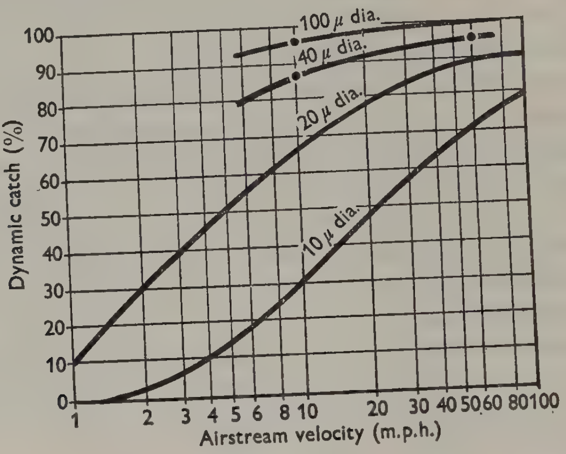
* It is preferable but not essential to employ a probability scale for the volume percentages (Yeomans, 1949) since it converts a sigmoid relationship to a straight line. The droplet sizes may be plotted on an arithmetical scale, but if the droplet spectrum extends into large sizes a logarithmic scale is preferable. In plotting the cumulative curve, it is important to take the upper limits and not the mid-diameters of the droplet size categories (Brown & Watson, 1953).

This boundary layer of air around obstructions through which small droplets fail to penetrate causes droplets smaller than 30μ in diameter not to be filtered by foliage; space sprays designed to penetrate through dense woodland should therefore have a droplet size of 10–30μ, as Hocking & Yeo (1953), Hocking, Parr, Yeo & Robins (1953), Yeo & Thompson (1954) have confirmed in recent work on tsetse fly control. When aerosols are emitted from generators on the ground, droplets of more than 40μ in diameter do not remain airborne for a sufficient distance to be useful as space sprays and for aircraft space spraying droplet diameters must not exceed 50μ.



Text-fig. 1. Dynamic catch of droplets of 10, 20, 40 and 100μ impinging on ⅛ in. diameter cylinder at various air speeds, according to Brooks (1947).

The filtering effect of the plant growth produced by impinging droplets is termed '*dynamic catch*' or *Em*, defined as the percentage of fractional width of the approaching stream which is cleaned of droplets (Brooks, 1947). This dynamic catch is in negative correlation to the M.M.D., in positive correlation to speed of the droplet and varies inversely with the diameter of the obstruction. Brooks (1947) has produced curves which are useful in deciding the diameter of droplets which still can be usefully employed for space sprays and at what velocity and what droplet sizes adequate deposition for cover-sprays can be expected (Text-fig. 1). A study of his curve shows that a dynamic catch exceeding 90% can be expected for droplets of 100μ diameter at a speed of about 3 m.p.h., while for droplets of 40μ diameter an air speed of approaching 20 m.p.h. is required to give a similar dynamic catch.

In sprays without air support the sections of the droplet spectrum comprising the smallest droplets of any herbicidal or insecticidal spray are therefore often not deposited and remain airborne; when they are moved outside the area to be treated by air currents, they are called spray drift.

Spray drift

The danger of wind drift of spray droplets during the spray application away from the area to be sprayed to neighbouring land is an important limiting factor in crop spraying. Weedkillers have caused many instances of damage by drift to neighbouring susceptible crops, but spray drift must not be confused with vapour damage. Certain herbicides evaporate when warm weather follows spraying or there is interaction between soil and weedkiller and clouds of herbicidal vapour are then moved to adjacent susceptible crops by air currents; great damage has been caused by this phenomenon, which is prevented by the use of phytopharmaceuticals which even under 'exceptional' weather conditions are not sufficiently volatile. The drift of toxic phytopharmaceuticals forms an unpermissible public health hazard on the downwind side of the spray operation.

The losses of spray material caused by drift are considerable, reduce the economy of the operation, and make it advisable to discontinue the spraying operation when the wind gets too strong.

The amount of spray drift is determined by the type of the droplet size spectrum, the wind velocity at the time of application, the distance from the nozzle orifice to the target and, in the case of spray blowers, the velocity with which the supporting air stream impinges on the target surfaces. That part of the droplet size spectrum which comprises droplets under 100μ diameter is the potential cause of the spray drift with sprayers *without* supporting air streams. Nozzles of such sprayers intended for use with phytocidal and toxic phytopharmaceuticals should be so designed not to produce droplets of less than 90μ diameter.

It has so far proved impossible to design nozzles with droplet spectra inside the limits of 100 and 300μ; at present spray nozzles which produce no droplets under 90μ give too coarse a spray even for weed control. Fraser & Eisenklam (1953) have shown that rotating disk sprayers are the only known device which shows promise of giving a narrow drop spectrum above 100μ diameter.

With the exception of the last-mentioned possibility there is at present no suitable liquid atomizer that gives droplets in the range of 100–300μ without also producing much finer droplets, and hence mechanical means have been proposed to protect satellite droplets from the wind; *wind shields* have been designed for ground sprayers in the form of cowls fitted over the spray bars, which have proved effective in an evaluation by Edwards & Ripper (1953), and are satisfactory in practical use in conjunction with nozzles used in weed control.

The prevention of spray drift by nozzles producing a spray supported by a strong air blast has been suggested; a suitable device (the Schütz-Berthoud Aerobarre) (Schütz, 1952) has made its appearance in the last year and is now under test.

A reduction in the amount of spray drift by aircraft sprayers is claimed to be caused by the reduction of wing-tip eddies through so-called *spill plates* which are flow guides fitted close to or at the tips of aircraft wings. When fitted to the lower airfoil of a Steerman boom-and-nozzle aerial sprayer, they resulted in a sharp cut-off in deposit at the edges of the swath. An even plateau of deposit density was obtained across the entire swath, falling sharply to almost nil within 10 to 20 yards at the edges. Excellent comparative plots with and without spill plates are shown in Elliott's report on spruce bud worm spraying (Elliott, 1952*b*).

Spray cover

In those crop-protection methods where a spray deposit is required, as in the application of contact herbicides, residual insecticides and all fungicides, the extent of cover is important. If the influence of the droplet size on the coverage is examined, and it is for this purpose assumed that the droplets are uniform in size, it is possible to calculate (*a*) the number of droplets per unit area for a given rate of application, and (*b*) the fraction of the area covered by the droplets at a contact angle of 90°. Table 1 gives figures for 1 gallon per acre sprayed uniformly on an ideal 'billiard table' surface; although this table has severe limitations since it is based on 'monodisperse' sprays and ideally uniform deposition, and neglects the effect of

Table 1. *Relation of droplet size, number of droplets and areas covered by 1 gal. liquid applied per acre in mono-disperse sprays on 'billiard table'*

Drop diameter (μ)	No. of drops per cm.^{2}	Mean distance apart in cm.	Fraction of area covered at contact angle = 90°
10	213,500	0·00216	0·266
20	26,700	0·00615	0·133
30	7,910	0·0112	0·0887
40	3,335	0·0173	0·0665
50	1,708	0·0242	0·0532
75	560	0·0425	0·0355
100	213·5	0·0685	0·0266
150	63·2	0·126	0·0177
200	26·7	0·193	0·01331
300	7·91	0·356	0·00887
400	3·33	0·551	0·00665
500	1·71	0·708	0·00532
750	0·56	1·34	0·00355
1000	0·213	2·16	0·00266

coincidences of droplets, it does bring out the important point that the fraction of area covered increases as the size of the droplet decreases.

The limit of smallness of droplets suitable for residual sprays is set by the resulting low dynamic catch unless strong supporting air streams are used, as discussed in the previous section. Field experience has shown that the optimum droplet size expressed in M.M.D. for coverage by ground sprayers without assistance by supporting air blasts, is from 150μ down to 80μ, provided that there is no drift problem. Sprays applied from aircraft and falling from 5 to 25 ft. with turbulence require a larger droplet, namely a M.M.D. of 100–200μ without assistance by air blast or helicopter downwash.

There is a further as yet hypothetical method of increasing the dynamic catch by giving very small droplets an electrostatic charge opposite to that of plants to be sprayed. If the droplets come within range, such attraction would clearly suffice to overcome the border layer effect mentioned above. Suitable equipment is under development, but there is as yet no published information on its performance.

Courshee, Daynes & Byass (1954) have drawn attention to the fact that lime sulphur sprays have a range of fungicidal influence around the speck of deposit of a droplet; they term the diameter of this biocidal range d. If the area covered by the spray residue of a droplet on drying is called S, they postulate that the ratio between the effective fungicidal cover and the actual cover by the deposit of the fungicide is $(S+d)^2/S^2$ and is a maximum for a minimum drop size. It follows that small drops may be valuable not only because their smallness improves the actual cover by the spray deposit for a given application rate, but also because the actual cover with the much increased surface of the droplet need only be small to obtain effective cover, and the deterioration in performance of a spray is therefore twofold as the drop size increases.

This is an interesting deduction, which not only applies to certain fungicides but also to insecticides with a local fumigation effect which is found in a good number of insecticides, for instance lindane and parathion. Courshee *et al.*'s conception of effective cover as compared with actual cover is of further heuristic value. The surface area over which a mobile insect moves in the time in which the uptake of the lethal dose is desired, is an analogous zone of influence around the speck of insecticidal deposit. In this case Courshee's diameter of zone influence d varies with the *mobility of the insect species*.

Thus we can explain the discovery of Norman & Joyce (1954) that the same insecticidal dose of DDT per acre will give a similar mortality of the cotton jassid *Empoasca lybica* whether applied as high-volume or low-volume spray, but its effect on the larvae of the whitefly *Bemisia tabaci* is very different, the high-volume spray being far more effective The jassid is very mobile, hence Courshee's area of effective cover, even in the case of sparse droplet deposition by low-volume spraying, still overlaps. In the case of sedentary whitefly larvae where d approximates to effective cover, there are large unsprayed areas between the sparse droplets of the low-volume spray and therefore large parts of the plant surface remain without any effective cover, while the much more densely located deposits from high-volume spray give a measure of control. Where the mobility of the pest is much less than that of its parasites or predators, a low volume applied by conventional hydraulic sprayers or mistblowers will, in comparison with a high-volume spray, become negatively selective, in other words kill many more beneficials than pests. If this effect is added to the phenomenon called Voleterra's 3rd law of fluctuation of two species living together (1931)—that of the disturbance of averages—sequels very inimical to the agriculturist's interest will ensue, which should not be held against chemical control of pests but understood as a wrong method of application of an otherwise satisfactory phytopharmaceutical.

As far as fungicides and contact weedkillers are concerned, Courshee's conception of the effective cover applies also to the re-suspension of spray deposit but quantitatively this phenomenon seems as yet unexplored.

Courshee's (1954) postulation that $(S+d)^2/S^2$ is a maximum for a minimum size requires—apart from the already mentioned limitation through the decrease of the dynamic catch with reduction in droplet size—the further qualification that volatility and the greater sensitivity of a very thin film to decomposition under the influence of light and weathering puts limits to the tenacity of the effective cover as the droplet size becomes smaller.

Types of spray required for the tasks of crop protection

The tasks of crop protection for which phytopharmaceuticals are used in liquid dispersion vary enormously and consequently the type of dispersion required can differ as much as smoke from rain.

The type of atomization required can be divided in accordance with the desired effective dispersion of the spray chemical as (1) an aerosol, (2) a deposit of a number of comparatively large drops on the vegetation, and (3) cover of fine droplets deposited on plant and soil in (*a*) space sprays, (*b*) systemic sprays, and (*c*) contact sprays.

(*a*) *Space sprays*

Space sprays are required to kill flying insects and the droplets must remain floating as long as possible. The dynamic catch of vegetation must be minimized. Droplet sizes between 10 and 30μ form a good compromise between maximum control and prolonged floating and have to be adjusted (i) for the size of the insect, while (ii) kept sufficiently small so as not to be filtered out too much by foliage. Examples are control of Trypetid flies in orchards and over seed crops, aerial curtain spraying against locusts high above the vegetation where there are no obstructions, and the control of tsetse flies in the forest where obstructions are plentiful.

(*b*) *Systemic sprays*

Sprays which are absorbed and translocated by the plant require a moderate dispersion. In the case of plant hormone weedkillers and systemic insecticides, the deciding factor is the final concentration of active ingredient per unit weight of plant. So long as the required quantity of the spray chemical alights on the plant it is not necessary to have a very good cover as the plant will equalize the distribution to some extent by translocation. As these types of sprays have drift hazards, it would be desirable in non-blast-assisted sprays that no droplets should be smaller than 100μ. The existing plant hormone weedkillers are at present sprayed by flat fan nozzles with a droplet spectrum which has an unpleasantly large number of droplets smaller than 100μ.

(*c*) *Contact sprays*

(i) *Weedkillers.* Contact weedkillers require a better coverage but some lose their selectivity if the spray pressure is increased. Therefore they are applied at the rate of 40–60 gal. per acre at pressures of 60 lb. and have a droplet spectrum between 50 and 600μ with a M.M.D. of about 350, using the D6 nozzle. Where higher pressures are admissible the Majestic nozzle at 200 lb. p.s.i. has a M.M.D. of 135μ.

(ii) *Fungicidal and insecticidal sprays* (*other than systemics*). Where a good cover is desired, sprays should have droplets as near a M.M.D. of 60μ as possible if air-blast support is available, and such dispersion is compatible with drift. If hazardous drift cannot be prevented and no air-stream support is available, then they should be as near above 90μ as possible with the majority of the spray mass in droplets between 90μ and 160μ and a M.M.D. of 130μ. These droplet sizes should be attainable with improved equipment, but at present most nozzles used on hydraulic sprayers have a much wider droplet spectrum and some nozzles have a M.M.D. higher than 130, e.g. the D6 nozzle at 200 lb. p.s.i. has a M.M.D. of 170μ. The M.M.D. of sprays used for fungicide application in this country is often increased to 350μ by the use of low pressure with consequent reduction in cover, and it is not surprising that the resulting control is poor.

To execute these tasks of crop protection, agricultural engineers, biologists, public health experts, physicists and agriculturists have developed a series of types of equipment for the dispersion of liquids, which have been arranged in Table 2 in accordance with the droplet size of the dispersion produced. The description of the dispersion in crop protection and in nature is listed, as well as terminal velocity, time of fall and drift; the latter have been taken from Brooks (1947). Examples of sprayers and the M.M.D. of the dispersion produced were added for each type of equipment where known, as well as the investigator responsible for the assessment.

Types of equipment

It is not easy to bring the large number of types of spraying and atomizing equipment into a system, and in the following an attempt will be made to group the equipment into: (1) hydraulic sprayers; (2) spray and mist blowers; (3) aerosol generators.

TABLE 2. *Dispersion of liquids in nature and in crop protection, their speed and drift, and equipment for their production*

Droplet diameter (μ)	Description		Tasks	Type of equipment	Terminal velocity (ft./min.)	Time to fall 10 ft. from rest (min.)	Distance carried in 3 m.p.h. wind	Examples		
	Nature	Crop protection						Equipment	M.M.D.	Investigator
3000	Cloud burst	—	—	—	1172	0·0145	3·8 ft.	—	—	—
2000	Heavy rain	Spray	Hydraulic and gravity deposition	Hydraulic sprayers with large jets	1041	0·0152	4·0 ft.	—	—	—
1000	Modest rain	Spray		Hydraulic sprayers with large jets	763	0·0179	4·7 ft.	—	—	—
500	Light rain	Spray		Hydraulic sprayers	421	0·0265	7·0 ft.	—	—	—
380	Drizzle	Spray		Hydraulic sprayers	313	0·0320	8·4 ft.	D 6 nozzle on high-volume low-pressure sprayer	350	Edwards
290	Drizzle	Spray		Hydraulic sprayers	229	0·0437	11·5 ft.	Teejet 65015 on low-volume low-pressure sprayer	285	Edwards
200	Drizzle	Spray		Hydraulic sprayers	142	0·0704	18·6 ft.	—	—	—
170	Mist	Spray mist		Hydraulic sprayers and spray blowers	120	0·0833	22 ft.	D 6 nozzle on high-volume high-pressure sprayer	170	Edwards
								RSM mist sprayer	167	Hepplethwaite
100	Mist	Spray mist	Deposition with air blast	Spray blowers and mist blowers	55·0	0·1818	48 ft.	Microsol	90	Brown & Watson
80	Wet fog	Spray mist		Mist blowers	37·9	0·264	70 ft.	NIAE blast sprayer	70	Courshee
50	Wet fog	Spray mist		Mist blowers	14·82	0·675	178 ft.	Husman sprayer	(S.M.D.) 40	Brown & Watson
33	Wet fog	Aerosol		Aerosol generator	6·46	1·55	409 ft.	Alaska aerosol	30	Brown & Mulher
								Dynafog	25	Brown & Morriso
20	Dry fog	Aerosol	Space sprays	Aerosol generator	2·37	4·2	1109 ft.	Tifa	17	Peterson
								Swingfog	12	Brown & Morriso
10	Dry fog	Aerosol		Aerosol generator	0·593	16·9	4452 ft.	Alaska aerosol	10	Brown & Mulher
5	Dry fog	Aerosol		Aerosol generator	·0148	67·5	3·4 miles	—	—	—
3	Smoke	Aerosol		Aerosol generator	0·072	139	7 miles	—	—	—
2	Smoke	Aerosol		Aerosol generator	0·024	420	21 miles	—	—	—
1	Smoke	—		—	0·0059	1686	84 miles	—	—	—
½	Smoke	—		—	0·0015	6750	388 miles	—	—	—

As far as possible, the equipment will be characterized according to the droplet sizes which can be produced, width or narrowness of the drop spectrum, and the speed with which the droplets impinge on the target or float in the air, the output in gallons per hour, and the prime mover and horse power required. The biologist finds himself still much handicapped by the lack of relevant data provided by the makers of such equipment. As these characteristics are essential for best use of the equipment, I would like to make a plea to manufacturers not to send a machinery specification to print without these data. If a manufacturer has not got the necessary test facilities, in this country it is best to request a test by the National Institute of Agricultural Engineering, Silsoe, Bedfordshire, who for a moderate fee produce, and if desired publish, an excellent test report.

(1) *Hydraulic sprayers*

The largest percentage of the agricultural sprayers in use are hydraulic sprayers because they were the first to be manufactured. All these sprayers essentially consist of a tank, often with an agitator, a pump, discharge points in the form of nozzles or jets, auxiliary equipment such as control valves, filters, strainers, pressure regulators, pressure gauges and suck-back devices to prevent nozzle drip. Hydraulic sprayers produce dispersions with M.M.D.'s from 150 to 500μ, and are used for the spraying of agricultural crops, orchards and shade trees for the control of weeds, pests and fungi.

An increase in pressure increases the emission rate, raising it by 25% for every 100 lb. p.s.i. increase e.g. the 650067 Teejet gives 0·055 U.S. gal. per minute at 25 lb., 0·11 U.S. gal. at 100 lb. and 0·22 U.S. gal. at 400 lb. p.s.i. The increase in pressure also causes an increase in atomization by increasing the number of small droplets at the expense of the larger ones. With the usual orifice size of 0·05–0·125 in. used in hydraulic sprayers, the droplet sizes increase inversely as the square root of the pressure; in other words, a drop in pressure from 800 to 200 lb., thus reducing the pressure by a factor of 4, doubles the droplet diameter from 200 to 400μ.

The speed of the droplet impinging on the foliage is caused by residual kinetic energy left over after the energy absorbed by the dispersion, or is just the terminal velocity which the droplets attain in free-fall.

Hydraulic sprayers are available in all sizes, ranging from those with an output of a few gallons per hour to giants delivering 12,000 gal. per hour. Hydraulic sprayers are operated by men, mounted on animals, used as self-propelled units operated by internal combustion engines; are lorry mounted, tractor mounted, or drawn by tractor or draft animals; mounted on a single-axle pneumatic-tyred trailer with a power-take-off from the tractor, or mounted on aircraft, and can therefore be classified into: knapsack sprayers, animal sprayers, orchard sprayers, agricultural sprayers and aircraft sprayers.

A great number of hand-operated hydraulic and hydro-pneumatic knapsack sprayers with a capacity of 3 or 4 gal. are in use. Hydraulic knapsack sprayers are favoured in areas inaccessible to power equipment or where the size of holding is very small. The spray liquid is expelled by a hand-operated, often double-acting, pump. In hydro-pneumatic knapsack sprayers either compressed air or gas under pressure is used to force liquid out of the tank. A high degree of atomization is achieved by employment of nozzles with a small orifice, and highly concentrated solutions can be sprayed. For example a simple hydraulic sprayer, which is being used extensively in tropical areas of the British Commonwealth, delivers 11·25 gal. per hour, absorbing $\frac{1}{16}$ h.p. at a pump speed of 35 strokes per minute. The droplet spectrum, according to Edwards (1953), has a M.M.D. of 160μ at a pressure of 40 lb. p.s.i.

Animal-borne sprayers have been designed for bullocks, camels and donkeys but no performance data seem to be available.

Orchard sprayers have been discussed and classified by Kearns (1945), who groups them into stationary spraying pumps which are a permanent installation of the orchard, and mobile units where the spraying pump and tank are moved in the orchards. One distinguishes between hand-operated and automatic sprayers depending on whether an operator is required to direct the nozzles. Most of these hydraulic orchard sprayers have piston pumps; the majority of these are the horizontal 3-piston pump, delivering at a rate of 1200–3300 gal. per hour, at a pressure up to 800 lb., and discharging through so-called jets or fog booms, by which is meant a number of nozzles operating together. The orchard sprayer with the largest output is a development by Dr Carman of the Riverside Experiment Station of the University of California (Pl. 7, fig. 1). This is a high-volume high-pressure sprayer for citrus plantations, capable of applying 1000 gal. per acre on dense citrus trees—an amount essential for the control of scales. Its pump is a multi-stage centrifugal pump delivering 7200 to 9600 gal. per hour at a pressure exceeding 600 lb., discharging through cyclic oscillating guns.

Turning to *agricultural* (*crop*) *sprayers*, we can classify them, in the first place, into high- and low-volume sprayers, and for this purpose a high-volume sprayer is defined as applying 60 or more imperial gallons per acre, medium-volume sprayer applying 20–59 gal. per acre and a low-volume sprayer as applying between 5 and 19 imperial gallons per acre, while spraying machines which apply less than 4 imperial gallons per acre are sometimes described as ultra-low-volume sprayers. Following Robbins, Crafts & Raynor (1952), agricultural sprayers can be grouped according to their working pressure into high-pressure sprayers, which operate at 125 lb. p.s.i. and over, and low-pressure sprayers, which operate at up to 124 lb. p.s.i.

As some of the crop sprayers have no provision for agitation in the tank, one has to differentiate between agitated and non-agitated spraying machines. Hydraulic agitation suffices for readily soluble or self-emulsifying material, but mechanical agitation is required for emulsions containing a high percentage of oil and heavy wettable powders. Hydraulic agitation requires a pump of considerably higher output than is necessary to supply the discharger devices; the excess flow is by-passed and forced back into the spray tank through a series of holes in a pipe laid on the bottom of the tank. Mechanical agitation is more efficient and requires a small fraction of the power necessary for hydraulic agitation.

Droplet data were measured by Edwards (1953) for a widely used low-volume, low-pressure, non-agitated sprayer delivering 210 gal. per hour at 40 lb. p.s.i., absorbing $\frac{1}{3}$ h.p. and, at 45 lb. pressure, delivering droplets with a M.M.D. of 285μ.

A high-volume, high-pressure, mechanically agitated drop sprayer designed for farmer use has a fast-running, 2-cylinder, totally enclosed piston pump, applying 1680 gal. per hour at a pressure of up to 200 lb., absorbing 4·5 h.p. and when using D6 nozzles at 60 lb. pressure, producing droplets with a M.M.D. of 350μ, and at 200 lb. pressure droplets with a M.M.D. of 170μ (Edwards, 1953).

High-volume application often produces run-off of the spray liquid and it was demonstrated as early as 1938 (Ripper) that low-volume application produces a higher deposit of the phytopharmaceutical per unit area of the plant surface than if the same amount of chemical is applied by high-volume spraying, thus permitting a saving of approximately 15–20% of the phytopharmaceutical in addition to a cheaper application cost.

Low-volume spraying, e.g. 5 gal. per acre with 650667 nozzles at 40 lb. p.s.i. is, however, sensitive to wind and the use of wind shields is advisable to prevent serious drift unless the application is restricted to days of low wind force (less than 5 m.p.h.).

Aircraft sprayers. Hitherto all air spraying has been carried out by aircraft which have been constructed for non-agricultural purposes. Most aircraft may be adapted for spraying provided that certain basic aerodynamic principles are observed.

For spray dispersion the down-draught of the aerofoil is of importance in that it imparts an initial downward force to the spray, especially for the smaller droplet sizes; this force is many times the terminal velocity of free-falling droplets. Down-draught forces originating from an aircraft wing vary directly with the magnitude of the induced drag and inversely with the aspect ratio, i.e. $(\text{wing-span})^2/\text{wing area}$. The use of flaps will sometimes improve the down-draught characteristics of aircraft giving greater penetration of spray droplets through the crop, but the right configuration for crop spraying and modern trends of passenger plane design diverge. Because of these special requirements for crop-spraying aircraft, aeroplanes for agricultural purposes are being developed in the U.S.A.

The first, the so-called AG-ship, had great simplicity of construction, ease of loading and ease of maintenance (Weick, 1954*b*). The performance included low-speed operation with a special high-lift wing having a powerful full-span flap. The pilot was given an unusually clear field of view, particularly forward and downward. Great efforts have been made to provide protection for the pilot in low-speed crashes. These were dramatically put to the test when the AG-ship collided with a power line pole before a meeting of the American Cotton Congress in June 1953 and was almost totally destroyed, while the pilot was uninjured.

Several new aircraft developments incorporating outstanding features of the

AG-ship have now reached prototype stage. During last summer the writer inspected two: the Air Tractor, a biplane using high-lift aerofoil sections with all wings identical, a gull section to increase forward visibility, flap ailerons and an open rear section of the fuselage to allow easy cleaning; all tail surfaces are identical and interchangeable. The aircraft is powered by a 400 h.p. engine, the spray tank is forward of the cockpit; the makers hope that the type certificate will allow a load carrying capacity of over 3000 lb. At present a prototype is flying. It is an interesting aircraft with many new devices, including spill plates on the wing tips (Pl. 7, fig. 2).

The other new airplane specially developed for fertilizer spreading in New Zealand, is a low-wing monoplane which in its configuration resembles the AG-ship with a high wing aspect ratio and a useful load of at least 1700 lb. using a 225 h.p. engine (Pl. 7, fig. 3). It is an all-metal plane and great care has been taken to produce a finish which resists corrosion. The hopper is on the centre of gravity behind the pilot's seat and the cabin fuselage has been stressed to 40 *g* so that in a crash at 75 m.p.h. the cockpit is not crushed and cannot sandwich the pilot between engine and load. This aircraft is in quantity production and in operation in New Zealand.

In the field of helicopters, a gallant effort was made here in Britain by the Ministry of Supply to develop a heavy load-carrying helicopter according to an agricultural specification, but this aircraft met with an unfortunate accident and the project has since been abandoned.

Helicopters have important advantages over aeroplanes for crop spraying because of their slower speed, their tighter and quicker turns, greater manoeuvrability and the ability to land close to the field to be treated. The disadvantage of contemporary helicopters is their mechanical complexity, which is responsible for a high first cost and high maintenance expenditure. The comparative costs of an aeroplane and helicopter of a load-carrying capacity of 7–8 cwt. is £2500 as compared with £35,000, so the cost of the ability to hover imposes a financial responsibility of £32,500. Nevertheless, under British conditions where so many fields are obstructed by trees and overhead wires, and the frequency of wind, the helicopter has over a number of years become the preferred tool for air spraying. Recent advances have been made in the production of a mechanically less complicated helicopter using ramjets (Payne, 1954*b*).

In America, subsonic ramjet helicopters are now flying. The Hiller Hornet was observed, which has not been designed for agricultural purposes but because of its short endurance would seem to be limited in its applicability to operations such as crop spraying. While the present model well proves the merit of the configuration, its useful payload would hardly seem to be adequate for spraying purposes. The disadvantage of the subsonic ramjet helicopter is the unavoidably high fuel consumption. As in all heat engines, the fuel consumption is inversely related to the compression to which the air is subjected prior to the release of heat by burning fuel in it. As the speed increases so does the ram compression of the air and with it the thermal efficiency of the ramjet.

The use of supersonic ramjets (Payne, 1954*b*) on helicopters promises an acceptable fuel consumption in addition to the mechanical simplicity of the ramjet installation. Paradoxically, a supersonic rotor is easier to design and manufacture than a subsonic one but flutter and cyclic control-response mechanism will require a lot of further attention.

These are relatively new aircraft which have not been assessed for air spraying. All work on the development of aerial crop protection has hitherto been carried out on non-purpose-built aircraft; the hydraulic air sprayers now in general use consist of a tank for the spray liquid, a pump driven either by a windmill or by an hydraulic drive from the engine. Rotary vane, centrifugal or gear pumps force the spray liquid at a pressure of 30–40 lb. through spray booms on which nozzles are fixed. An aircraft sprayer for which we have performance data is the Sprayster, giving through D6 nozzles a M.M.D. of 240μ at 40 lb. pressure. Droplets impinge at terminal velocity or are accelerated through downwash with quarter flap; output is 780 gal. per hour and the pump absorbs on windmill 2 h.p.

Knowledge of the performance of stationary spray nozzles cannot be applied without correction of their performance to aircraft, because (1) additional energy of atomization is added by the rapidly moving air; (2) the nozzle location and orientation of orifice of the nozzles has considerable effect on the droplet spectrum of the spray and the recovery of aircraft sprays (Kruse, Hess & Ludvik, 1949).

Of the following three droplet size ranges, only the second and third are achieved by hydraulic sprayers:

(i) The finest dispersion (10–50μ) presents a tremendous number of droplets produced, and is useful for space sprays; it provides the widest swath width (260 ft.) but is very sensitive to adverse weather conditions.

(ii) The 50–100μ range appears on theoretical grounds to be the best compromise between dynamic catch and swath width (200 ft.) and is not so sensitive to adverse weather conditions.

(iii) The 100μ and larger particle size range obviously gives the best dynamic catch and is the least affected by adverse weather. It represents the fewest droplets produced, gives less safety factor on distribution over the swath width, and provides the narrowest swath width (120 ft.).

When forests are to be penetrated, as for instance in tsetse fly or mosquito control, only the first range (10–50μ) is effective, and the preferred range is from 50 to 30μ.

The control of locusts by aerial curtain spraying (Sawyer, 1950; Wootten & Sawyer, 1954) has special requirements, as it is a case of space spraying where slow subsidence rates are desirable. A particle size range of 50–100μ is an immediate objective for this application.

Helicopters possess a down-draught of high magnitude which favours dispersion (Maan, van Bemmel, Milborn & Ten Houten, 1948; Maan, 1949; Ripper & Tudor, 1948), recovery of smaller diameter sprays, and deposition on the lower surface, of leaves. For rotor downwash the droplet range selected of 50–100μ would be ideal for fungicide applications, but in fact much larger droplets are being used. Where larger sizes are used, the number of droplets produced should be increased by increasing the volume discharged and lowering the concentration of the active ingredient.

An increase in air speed decreases the size of the droplets and results in a finer droplet spectrum, but also decreases the swath width. The lowest practical air speed will give the greatest swath width. The orifice size of the nozzle has little influence on the spray pattern and a nozzle arrangement which gives a satisfactory swath pattern with one of the nozzle types, will also give a satisfactory spray distribution with another.

The direction of the nozzles in relation to the direction of flight is of importance; experiments by the U.S.D.A., U.S. Public Health Service, Kruse *et al.* (1949) of the Malaria Control Branch of the Tennessee Valley Authority, and Edwards (1953) in this country have all shown that in experiments with nozzles in the trailing, forward and downward direction, the smallest mass median diameters were produced by nozzles directed forward into the slipstream, intermediate when directed downward, and largest when directed towards the rear. Edwards (1953) has shown that M.M.D. decreases if the direction of the nozzle is changed from the downward position via 45° forward to 90° forward, and in experiments carried out on an Auster using D 6 nozzles, he recorded for the downward position a M.M.D. of 225 μ, while at 45° forward it amounted to 160 μ, and at 90° forward to 150 μ. These observations are in accordance with the formula for atomization of liquid by Nukiyama & Tanasawa (1938–40) which has regard to the fact that the break-up of liquids after they leave the orifice is due to the interaction of liquid and air and proportional to the differences in velocity between the two.

The influence of nozzle direction under helicopter conditions has been investigated by Kruse *et al.* (1949) for speeds between 20–80 and 180 m.p.h. The droplets issuing from nozzles directed forward became smaller in diameter as the speed increased, while droplets from nozzles pointing in the trailing direction increased in diameter as the speed increased to a point near 80 m.p.h., where the liquid velocity was equal to the air velocity. After this point the droplet diameter varied inversely with the speed, but in the experiment was always larger than obtained in forward direction.

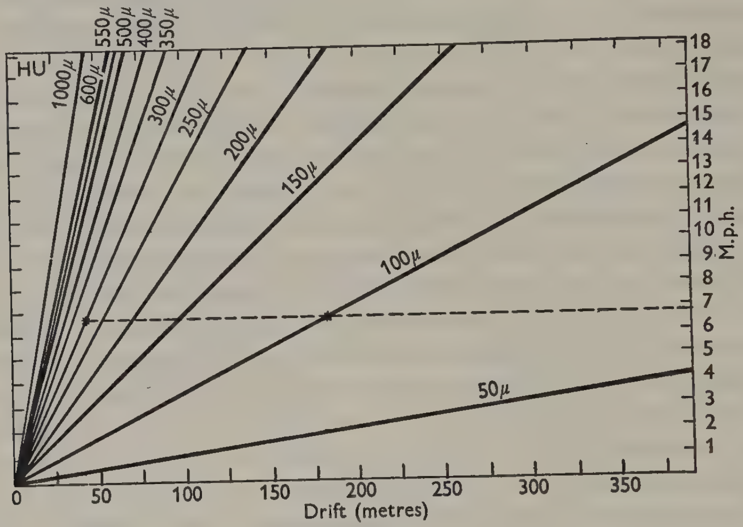
Summing up our knowledge of factors determining droplet size of spray produced by nozzles from aircraft, we find the droplet size can be altered by four factors: (i) physical characteristics of the liquid; (ii) discharge pressure; (iii) nozzle orientation; (iv) speed of the aircraft.

Direct spraying and drift spraying by aircraft. Aircraft are often used like ground sprayers, flying during spray runs in close proximity to the ground, but even under these conditions the slip stream increases the swath width to about 5 times the width of the spray bar. In many cases this *direct spraying* is still the only feasible use of aircraft and in this application the spray patterns is of great importance; it is thought that trapezoid and triangular spray patterns are less sensitive to imperfect spacing. Weick & Roth (1954) have established that the factors which affect spray pattern are: (*a*) nozzle location, (*b*) application height, (*c*) wind, (*d*) air speed. Owing to the air flow around the fuselage and the propeller slipstream an unequidistant nozzle spacing gives the desired spray pattern and for the various types of aircraft the right distances have been worked out empirically. The displacement of spray pattern from the various nozzles under the influence of a cross-wind is not constant and the displacement is smallest for the nozzles nearest the centre of the aeroplane and largest for the nozzles near the wing tips. At a low wheel height above the ground of 3 ft. the effect of a cross-wind is not great and is nearly constant for different nozzle locations across the span, but at 7 ft. height the displacement of the pattern due to the cross-wind is greater and the nozzle pattern at the wing tip is moved twice as far laterally as those near the aircraft centre. The effect of cross-wind, which is probably the largest and least controllable of the factors which influence spray distribution, complicates the achievement of uniform spray density in the swath when operating under varying wind conditions using the direct spraying method (Roth, 1954*a*, *b*).

When spray chemicals are released at greater heights, a wider swath width is obtained with one flight across the target. This principle—known as the *Porton method* or *drift spraying*—has been developed at the Civil Defence Establishment at Porton and at the Suffield Experimental Station of the Defence Research Board in Canada; it has been explored for crop protection purposes, initially in connexion with locust control, by Gunn, Perry & others, (1948); Gunn, Lea, Botha, Callaway, Clackson, Immelman, Taljaard & Ward, (1948).

Important advances in drift spraying have been made by Brown (1954) in Canada, developing mosquito and *Simulium* control. Drift spraying is based on the principle that if an assortment of droplets is released into the air, they fall and accelerate under the influence of gravity, and reference to Table 2 shows that the different droplet sizes are carried in the wind for varying distances. The fall of droplets through gases or liquids which flow around them in a viscous manner is governed by Stokes's Law. The viscosity of the air through which the droplets fall sets a limit on the maximum speed they can attain, which becomes the constant rate of fall, or terminal velocity, which in turn is determined by the ratio of the droplets surface area to its volume. The larger the droplet, the closer will its velocity approach conditions known as free fall. Thus when a spray consists of a number of droplet sizes and is emitted into a cross-wind, the largest droplet will fall fastest and will therefore deposit closest to the aircraft track. The distance which the droplets fall will thus prove proportional to the product of the speed of the cross-wind and the height from which the droplets fall. This product is known as HU, is expressed in unit feet of miles per hour, and can be calculated for any direction of the wind with respect to the direction of the flight. The cross-wind component U is obtained by multiplying the speed of the wind by the cosine of the angle θ by which it diverges from the cross-wind. Amsden (1954) has applied this principle to the control of the cotton jassid *Empoasca lybica* in the Sudan. Text-fig 2 shows a chart used to calculate the drift for a given droplet spectrum and a known cross-wind component.

When fields are to be sprayed, parallel runs are made at intervals dictated by the intensity of the deposit to be obtained. Applications are made from such height that the *HU* product is large enough and the swath therefore wide enough to overlap. There is nearly always enough cross-wind component in the wind obtaining at the time for drift spraying, but this application method is no longer recommended if the wind is less than 15° angular distance from the track.



Text-fig. 2. Relation between height-wind speed (*HU*) and drift of droplets of 50, 100, 150, 200, 250, 300, 350, 400, 500, 550, 600 and 1000 μ, according to Amsden (1954).

While aircraft spraying against the cotton jassid in the Sudan has hitherto been carried out by direct spraying on a track width of 65 ft., Amsden has shown that satisfactory kills can be obtained by the drift-spraying method at track widths of 210 ft. There are obviously great merits in this method, provided that sufficiently large areas are to be treated, which in this country, for instance, occur in forest spraying.

(2) *Spray and mist blowers*

Spray blowers are devices by which the spray liquid is wholly or partly hydraulically atomized and then carried to the target by an air stream which passes the source of the spray. The term *mist blower* should be reserved for devices by which the spray liquid is finely dispersed by means of airblast nozzles or spinning disks and the resulting mist is then carried to the target by an air stream in the same way as with spray blowers. The difference between spray and mist blowers is therefore substantially in the degree of dispersion and in the atomizing equipment which produces this dispersion. Both types of applicators cause emitted droplets to impinge on the target at a considerable speed. When the dynamic catch was discussed, it was pointed out that an increase in the speed at which the air droplets hit target surfaces increases the deposition of smaller droplets. Through the greater speed of the droplets imparted by the spray or mist blower's air stream, it is possible to reduce considerably the volume of spray chemicals and use correspondingly lower volumes of spray liquid at higher concentrations. Highly concentrated sprays avoid the disadvantages of having to use large quantities of water, and there are in addition savings in the quantity of chemicals required, for reasons already mentioned under low-volume application with hydraulic sprayers.

Spray and mist blowers can be classified into those which have axial-flow blowers of the turbine type and the centrifugal fans with rotary flows of the squirrel-cage type; no specific type is best for all conditions.

In spray blowers the liquid is broken up in hydraulic nozzles to which the liquid is either propelled through pumps or by pneumatic pressure, and the liquid is dispersed through single nozzles, or banks or rings of nozzles. The air passes these nozzles at considerable speed (between 100 and 259 m.p.h.) and then carries the liquid to the target area; in general, very small spray blowers utilize high-velocity air to break up the spray by a shearing action, hence they use a high-velocity, low-volume, single- or double-stage fan. The medium and medium-large spray blowers employ a combination of air velocity of 125–170 m.p.h. and hydraulic pressure of about 150 lb. or less to atomize the spray. Equipment of this type has a delivery of 4000–10,000 cu.ft. of air by either of the two types of fans mentioned before. For tall trees an air velocity of 120–150 m.p.h. is required in volumes of at least 8000 cu.ft. but volumes of 1200–1500 cu.ft. at velocities of 125–135 m.p.h. are preferred for tall trees up to 70–120 ft. (Potts & Garman, 1950; Potts *et al.* 1950).

An optimum ratio exists between velocity of the air stream and diameter at the orifice to attain the greatest height and distance with a given horse power. The volume of air delivered is directly proportional to the square of the diameter of the outlet.

The size, shape and flexibility of the outlet are very important; outlets are either round or spreader outlets designed to spread the mist. For the latter purpose, multiple round outlets or fan or fishtail-shaped outlets with or without spreader partitions, fins or vanes are used. For the largest machines the outlet should be so designed that the shape and width of the air stream can be quickly changed even while the machine is operating and moving and without affecting the droplet size. Thus it is possible to change the velocity of the air stream and apply a wide 'soft' air-spray stream to trees close to the spray blower and then suddenly change to a narrower high-velocity stream to attain greater height and distance. Air velocities of 120 m.p.h. at the outlet are desirable for orchard shade tree and row crop work, and velocities of 150–170 m.p.h. have given satisfactory results for orchard and shade tree work. The orifice velocity of the spray-laden air stream on a mist blower is much higher than the velocity at which it impinges on the target, which Potts termed 'deposition velocity'. Potts *et al.* (1950) have compiled a useful table of air velocities at various horizontal distances from the blowers which is produced as Table 3. The deposition velocities have to be selected in accordance with the droplet sizes to be used and a reference to Text-fig. 1 will give the dynamic catch to be expected.

According to Yeomans, Rogers & Ball (1949) the minimum air velocity for efficient deposition is 2·2 m.p.h. for 50μ droplets on a sprayed object of ¼ in. diameter, and 16·2 m.p.h. when the objects are 2 in. in diameter. For 100μ droplets the optimum air velocity is calculated to be 1·1 m.p.h. for 1 in. wide objects, and 4·6 m.p.h. for 2 in. wide objects.

TABLE 3. *Air velocities at horizontal distances from mist blowers to show deposition velocities, according to Potts* et al. (1950). *Delivery from round outlets of given diameters.*

Diameter of outlet (in.)	Approx. volume (C.F.M.)	Velocity (m.p.h.) at the following distances from blower							
		At blower outlet	10 ft.	25 ft.	50 ft.	75 ft.	100 ft.	150 ft.	200 ft.
1	140	300	15	2	0	—	—	—	—
1·25	200	225	20	3	0	—	—	—	—
2	370	200	30	5	1	0	—	—	—
4	1,300	170	40	8	2	0·2	0	—	—
8	3,800	125	40	10	3	1	0	—	—
10	6,100	140	70	35	6	3	1·8	0	—
10·50	6,300	140	75	40	7	3	2	0–1	0
12	7,500	125	60	30	7	4	2·5	1	0
24	20,000	90	50	25	7	5	3	2	0
24	28,000	120	75	40	17	10	7	5–7	3
54	27,000	50	35	30	8	4	3	2	0

Tank and agitation. Supply tanks vary in size depending on the capacity of the equipment and the nature of application. 40–75 gal. are used for shade trees and 75–300 gal. for fruit-tree work. An agitator is desirable which should move slowly and sweep the bottom of the tank because it deals with concentrated suspensions. The tank must be made from a non-corrosive material or treated with an epoxy or phenolic enamel which stands up to oil solvents and spray chemicals.

Spray blowers. Spray blowers differ from mist blowers in that they have hydraulic nozzles and pumps. The nozzles must be capable of atomizing concentrated mixtures of spray chemicals and clogging must be avoided; orifices should not be below $\frac{1}{16}$ in. in diameter. Strainers and clean non-corroding tanks are essential. As the abrasion by the spray concentrates is formidable, hardened steel is used for nozzles up to a pressure of 29 lb. and hardened stainless steel above this pressure. Whirl-chamber nozzles have been found satisfactory. Nozzles must be placed in the air stream to obtain a maximum dispersion by the air and should be spaced in such a way that the spray droplets are distributed throughout the air stream with as few nozzles as possible in order to use the biggest possible orifices.

For single air outlets of less than 7 in. diameter, a single nozzle is used pointed against the air stream or at right angles to it because placing the nozzle in the same direction as the air stream gives coarser atomization. In the case of multiple outlets, one nozzle per outlet is provided. For larger outlets such as 12 in. diameter, four nozzles at right angles to the air blast are usual. Pumps are plunger, centrifugal or gear type.

One of the earliest successful spray blowers is a fair-sized orchard sprayer where the volume can be altered between 50 and 500 gal. per acre. These spray blowers are available in various sizes, ranging from 60,000 gal. per hour down to 12,000 gal. per hour. The air stream moves 20,000–125,000 cu.ft. per minute at 10 m.p.h., but there are similar types also produced for smaller trees and hops. All are tractor-mounted and equipped with engines of 42 h.p.; the nozzle pressure is 50–70 lb. p.s.i. but no droplet size data are available.

A British spray blower operating at higher wind velocities at 3–50 gal. per acre produces a pneumatic atomization of the spray liquid and hydraulic atomizations at 50–250 gal. per acre. The fan moves 10,000 cu.ft. per minute at a speed of 112–160 m.p.h., while the atomization of liquid is effected at 30 lb. pressure. The sprayers are tractor-mounted and absorb 25 h.p. Again, no droplet data are available.

The biggest sprayer of this kind has been produced by Dr Carman at the Riverside Experiment Station for use on citrus trees. It is equipped with a squirrel-cage fan, 36 in. in diameter, which is capable of delivering more than 40,000 cu.ft. of air a minute and has a centrifugal pump. The lateral distribution of air through the vertical 'fishtail' outlets aids in distributing the spray emitted under high pressure from nozzles distributed throughout the length of the air opening. A hinged section of the outlet is oscillated forward and backward and the resultant change in air flow generally proves useful in moving leaves and small branches at the periphery of the tree and favours penetration of the spray into the inside portions of the trees. Low gallonages of 100–200 gal. per acre can be applied effectively as well as amounts up to 1000 gal. Droplet size assessments of this very interesting machine are as yet not to hand.

An important spray blower is the slow and low-flying helicopter sprayer, in which the spray dispersion is produced hydraulically by a power-driven gear or centrifugal pump, pumping the spray liquid out of two pannier tanks totalling 60 gal. via a pressure regulator to two spray bars, of a total length of 30 ft. equipped with thirty-four nozzles. The output is 1380 gal. per hour. The M.M.D. of D6 nozzles was measured as 260μ at a pressure of 60 lb. p.s.i. The spray droplets issuing from the spray nozzles are carried in the helicopter downwash at a speed of 30 m.p.h. towards their target; as long as the helicopter flies in its ground cushion, i.e. in a distance from the ground of less than its rotor diameter (Ripper & Tudor, 1948), there is considerable deposition velocity of the air stream and rebounding of the spray-laden air near the soil takes place; hence considerable deposition on lower surfaces of the leaves is obtained.

Mist blowers. Mist blowers are devices by which an air stream is used not only to carry the spray mist, but the spray liquid is also atomized by an air stream or rotating disks. Mist blowers are often called atomizers, but as physicists use this term for any disperser of liquid, the term mist blowers would seem more accurate. The droplet sizes produced by atomization of liquid in an air stream are much smaller than those resulting from hydraulic dispersion and are in a range of 40–100μ. We are thus entering with mist blowers into a different type of dispersion.

There are a large number of mist blowers; the oldest ones are based on the principle of the air-blast nozzles—an air stream is moved past the orifice of the liquid and shears off liquid particles and then the droplets are either carried by the same air stream or by a supporting air stream of lower velocity. Hollow jets or shear-type nozzles are supplied with liquid at 3–6 lb. p.s.i. and air velocities of 150–250 m.p.h. The droplet size can be varied by changing the direction of the jets relative to the direction of the air blast. Jet orifices of $\frac{1}{6}$ and $\frac{3}{32}$ in. are frequently used and the discharge ends of the jets are sharpened to increase the shearing action. Lately an interesting air blast atomizer has been developed by Hoare of the National Institute of Agricultural Engineering which has been described by Courshee *et al.* (1954). This device consists of a number of jets for the liquid, each of which is surrounded by a tube through which air passes under pressure of 18 lb. These air jets are fed by a compressor and the resultant droplets are carried by an air stream produced by a squirrel-cage-type fan to the target. The droplet range produced has a M.M.D. of 70μ.

A similar device is the Husman sprayer which, according to Brown (1951), produces droplets of a M.M.D. of 47μ at setting 10 lb. p.s.i. It uses the spraying system air-mix nozzles (no. 120-6-36-60 air combined with no. 4010 liquid in assembly no. 30) and the air stream is produced by a rotary vane compressor supplying 8·3 cu.ft. per minute at a pressure of 8–15 lb. p.s.i., powered by a 1$\frac{1}{4}$ h.p. engine.

In Brann's mist blower (1951) the liquid emerges from a circular clearance of 0·001–0·003 in. on a spring-loaded gland and is then sheared off from the gland by an air stream of 400 cu.ft. per minute. The orifice of the mist blower is mounted on a revolving head rotating at 15 r.p.m. This mist blower can be used for fruit tree spraying; it stirs up the air effectively and turns leaves over so that deposits on both sides can be obtained (Pl. 7, fig. 4).

A number of mist blowers use atomization by air blast of considerable velocity shearing the liquid off stationary shear plates. These are of varying size, either single knife edges or aerofoils. In one such device, the makers state that the air stream passes the shear plate at a speed of 250 m.p.h. These mist blowers are made in a great range of sizes, from small shoulder-mounted atomizers to trailer-mounted large machines requiring 11 h.p. and having tanks of 100 imperial gallon capacity.

The small shoulder-mounted mist blowers (Pl. 8, fig. 2) are of great importance for tropical areas; while the atomization is satisfactory, a disadvantage might well lie in the careful attention which the small internal combustion engine requires but does not always get in the hands of agricultural labour in backward countries.

Mist blowers have been used for crop protection tasks in orchards and hopyards and for shade trees, but their employment for field crops is still in the development stage. The normal practice in row crop spraying of using one to three hydraulic nozzles per row cannot be employed with mist blowers because the output of the standard mist blower outlet is too large. The development has therefore taken two divergent ways; Schütz (1952) has abandoned the conventional mist-blower outlet and injects spray liquid into horizontal cylindrical tubes of 3 in. diameter through jets which are varied in accordance with the output required. These tubes have stream-straighteners in the form of a tube-shaped grid and into these tubes is also introduced an air stream of more than 100 m.p.h. which issues on to the crops through a number of vertical nozzles having an acorn-like shape and serrated shear surfaces around the orifices at their tips. The spray liquid is sheared off by the air stream and the inventors claim that a uniform layer of spray liquid is important on these shear surfaces. This is ensured by an equalizing recess in the basal part of each outlet. Droplet size investigations on this mist blower are in progress.

The other line of mist blower development for ground crops makes use of the conventional mist-blower outlet but the emission is distributed over much more than one row. This is achieved in two ways: in the first the outlet is directed at right angles to the direction of travel of the mist blower and often also upward. The mist blower emits its droplet-laden air stream in a flat trajectory and the droplets fall out of this stream, whereby the larger droplets are deposited nearer to the sprayer and the smaller droplets are carried farther away.

If this operation is carried out with the wind it constitutes a form of drift spraying but in neither case is an even cover obtained because of the winnowing effect. The deposit is adequate for the control of mobile insects where a good cover is not required and has been used successfully against grasshoppers, fleabeetles, locusts and leafhoppers. It is obviously very wind-dependent and easier used on land where crops are not grown in rows. If the mist blower is used so that the trajectory of the mist-laden air is not downwind, the operation cannot be carried out at wind velocities above 3 m.p.h. This difficulty is partly overcome by the second method in which the more conventional mist-blower outlet is directed forward or rearward of the direction of travel of the implement and slightly downward. This is effected by manifolds with three to five round outlets, one large slot or fishtail outlet with spreader vanes, or three to five smaller fishtails or slot outlets (Potts *et al.* 1950) or by rotating or oscillating outlets which sweep the area to be treated. Brann has developed at Cornell University the last-mentioned modification by providing on his mist blower a rotating head with a governing valve so that the liquid is only turned on in the outlets when they traverse an arc of 120°, namely 60° either side of the direction of travel. For this purpose a valve is provided in the rotary head so that the liquid is only fed by means of a valve selector to those of the oscillating outlets which are on the top and point forward within an arc of 60° either side of the direction of travel, so that the liquid is dispersed only by nozzles when discharging forward. It is an interesting experimental unit which has not been completely assessed (Pl. 7, fig. 4).

Considerable attention has been given to mist blowers where atomization is effected by spinning disks and then carried in an air stream produced by a fan. The spinning disk is either power-driven or driven by a turbine actuated by the air stream. In this case the insecticide is mechanically atomized by being thrown off the periphery of twenty-one spinning disks of 8½ in. diameter rotating at 8125–9750 r.p.m. One model has a power requirement of 7½ h.p., and an emission rate of up to 250 gal. per hour is claimed by the makers. The resulting mist has, according to Brown & Watson (1953), a M.M.D. of 71 μ at a setting $\frac{1}{16}$ in. open and 90 μ at a setting of ¼ in. open.

The turbine-driven disk atomizers are similar in operation, but their speed of rotation and therefore droplet size obtained is dependent on the rate at which the turbine can extract power from the air stream. All atomizers and 'aerosol generators' of this type produce a fine mist-like spray and not an aerosol, in other words the droplets have a M.M.D. above 40 μ; the production of much finer dispersion with a M.M.D. of the droplets of less than 40 μ has confronted the nozzle designers with difficulties.

(3) *Aerosol generators*

These difficulties were overcome in the aerosol generators which are devices which produce an aerosol, i.e. a dispersion of liquid with a M.M.D. of less than 40 μ.

We have in our review of equipment now arrived at a size of dispersion where the surface-volume ratio is much larger and where the terminal velocity is a few feet per minute. The first break-through into the true aerosol field by crop-spraying equipment suitable for outdoor work was made with thermal aerosols.

Thermal aerosol generators are based on the principle that liquid phytopharmaceuticals or their oil solutions are finely atomized by blasts of heated air or exhaust gases. The shatter afforded by the high-velocity blast is enhanced by the effect of the heat in decreasing the viscosity of the phytopharmaceutical, and the droplet size is further reduced by the vaporization of the oil which occurs before the aerosol is emitted into the outside air where recondensation of the gaseous phase of the phytopharmaceutical occurs. Hot-gas aerosol generators have given good results for aphis control and also a number of other agricultural applications. Exhaust aerosol generators (Jones & Holton, 1949) have been somewhat superseded by special equipment which in two cases were started as projects outside crop protection appliances.

One insecticidal fog applicator is a development from a naval fog generator. An oil solution of the insecticide is atomized into an air stream of 150 cu.ft. per minute at about 1000° F. through nozzles at a pressure of 25–30 lb. p.s.i. The power for the air-blower fuel pump and insecticide pump is supplied by a $6\frac{1}{2}$ h.p. engine. The droplet size of the cloud of aerosol can be varied by a particle size selector, and a good analysis of droplet data has been produced by Peterson (1952). At a selector setting of 10·2 a M.M.D. of 17μ is obtained. There may be some decomposition of the insecticide at this heat, amounting in the case of DDT to about 30% in oil solution and 50% in oil emulsion.

This fog applicator has given promising results for space sprays in orchard and vineyard work against mobile insects which were present at the time of application, but is not successful in obtaining residual deposits and is useless for weed control.

The other interesting thermal aerosol generator was originally developed to start aero engines in cold weather. The tool gives a narrower droplet spectrum than the fog applicator and has as its main advantage its light weight and portability. It operates on the principle of a pulse jet as used in the V 1 robot aircraft. The pulse jet produces a stream of hot exhaust gas into which the phytopharmaceutical is injected (Plate 8, fig. 1). The phytopharmaceutical is evaporated and a re-condensation takes place when the exhaust emerges into the atmosphere, and results in a dense fog. A series of fuel-air charges are fired in a combustion chamber and the depression following each peak pressure wave is utilized for drawing in a fresh charge via a non-return valve. The exhaust gas moving at high velocity escapes through a discharge pipe and continues to flow after the initial thrust that started the movement is no longer present. For this purpose there is connected to a pear-shaped combustion chamber fitted with an exhaust pipe, a tube carrying a non-return valve and a carburetter; the end of this tube is closed with a glow plug which extends into the combustion chamber. The initial fuel charge is fired by the glow plug which is connected to a 6 V. battery which is disconnected once the machine is started. The machine then operates at 80 pulsations per second. It supplies the insecticide under a pressure of 6 lb. p.s.i. at the rate of 2 gal. per hour and gives, according to Brown & Morrison (1955), an aerosol with a M.M.D. of $9-17\mu$. The distribution frequency is unimodal and extremely fine.

In another tool, designed on a similar basis, the insecticide is injected into the exhaust of a pulse jet engine operating at 83 explosions per second (Brown & Morrison, 1955). The output of this equipment is 5–9 gal. per hour but the droplet spectrum is wider because the machine produces a mixture of extremely fine droplets being re-condensates, together with a second mode which is coarser than true aerosol droplets.

Another type of thermal aerosol generators uses steam. The insecticide is atomized into the steam coil as it leaves the chamber at a temperature of 500–700° F. and a pressure of 100–150 lb. p.s.i. Steam and insecticide which is pumped at 30–45 lb. p.s.i. meet in a single nozzle. The power is supplied by a $1\frac{1}{2}$ h.p. engine and the water consumption for steam raising is either 40 or 80 gal. per hour. Although it is an aerosol generator, many of the droplets emitted fall into large-size classes with a resulting high M.M.D. of 26μ at setting 4 and 700° F. at an emission rate of 40 gal. per hour (Brown & Watson, 1953).

A survey of thermal aerosols would be incomplete without mentioning insecticide smokes, which are produced by igniting and burning insecticide mixtures with some slow-burning materials. When DDT or BHC is used as the active ingredient there is a decomposition amounting to about 30%; these are good as space sprays but show only slight penetration of crevices. Results obtained with smokes in the field have, on the whole, been far less satisfactory than those obtained indoors, but 1 lb. canisters have been used to kill tsetse flies in the bush and ravines not easily accessible by aerial spraying.

Thermal aerosol generators were until recently the only practical means of economically producing true aerosols outdoors. It has now been shown that the aerosol atomizer as developed by Wilson (1950, 1951) of the U.S. Public Health Service at Anchorage, Alaska, not only equals but even exceeds in fineness the dispersion produced by thermal aerosol generators. Brown & Mulhern (1954) showed that this aerosol atomizer is capable of producing droplets of a M.M.D. between 5 and 30μ depending on the viscosity of the oils. A M.M.D. of 5μ was achieved with light fuel oils of very low viscosity, while heavy diesel oils such as are burned in locomotives produced 30μ.

The aerosol atomizer is a device which consists of a great number of simple air atomizers, comprising a tube extending horizontally to abut on a vertical tube which ejects the liquid, often known as the flit gun principle. There are five sections of 12 in. of which the air tubes have a diameter of $\frac{3}{4}$ in. and the liquid tubes a diameter of $\frac{1}{2}$ in. Each section has sixteen orifice tips, so that all told there are 80 in the aerosol generator. The bore of the liquid emission tips is 2·7 mm. and the air outlets 5·4 mm. and each air outlet dispenses 1 cu.ft. per minute per nozzle at 40 lb. p.s.i. which is produced by a 33 cu.ft. per minute compressor, and the five sections atomize 15 gal. per hour. The device was originally conceived for mosquito control, but is indeed an important development which will have wide applications.

In our survey of spray dispersion we have now reached aerosols of droplet sizes which will only deposit on vegetation readily when impacted by great speed or are attracted by electric charges. The very great number of droplets into which the phytopharmaceutical is dispersed and the enormous surfaces of dispersion of this type, offer very interesting possibilities which will be explored in the future.

VI. APPLICATION INTO THE SOIL

Soil fumigators have been designed to inject soil fumigants into the soil to a depth of 3–8 in. in lines 10–18 in. apart. The simplest equipment, a hand injector, comprises a syringe of 1 gal. capacity which delivers 1–15 cc. of liquid fumigant per plant. Hartley and Edson have tried to improve this device for the application of very toxic insecticides, and Edson's soil injector modification has been tried on a large scale in the tropics for the application of the systemic insecticide dimefox; there is, however, scope for further developments to make this equipment more foolproof.

Little progress has been made with larger soil applicators. A series of six to ten injector pieces or drills arranged on a boom are supplied with fumigant from a tank, either by individual pumps or by one pump using a distributor. An alternative method of injecting fumigants into the soil is combined with cultivations; the soil fumigant is metered by pump hose lines to pipes secured behind each plough share.

The application of systemic insecticides of high toxicity has stimulated the development of several devices. One such development has been described by Lane (1954) (Pl. 8, fig. 3). To a standard hop-spraying machine there are fitted two rear outlets capable of applying a jet of liquid directly to the hop hill; an ingenious single-way flap valve is opened by contact with the base of the hopbine or other obstruction and produces a spout of liquid to the base of the obstruction.

This single-way flap valve is fitted to the base of the tank which is rear-mounted, and attached to the valve is a length of brass wire. This wire comes through the middle of the tank, is looped over and attached to a pulley at the top of the tank. A rod runs down the whole way of the side of the spraying machine and at the bottom of the rod there is a contact finger; there is also a corresponding lever to which is attached the above-mentioned hinged flap. When the finger comes up against the bine it is pushed back, moves the pulley and brass wire, and opens the flap valve for a moment. At the same time that the flap is opened, 1 pint of liquid passes through the orifice.

Another way to apply systemic insecticides is to use water-soluble capsules of gelatine and similar products which are reasonably stable when kept dry in a container but which, if put in the soil, disintegrate through the moisture in the soil. Hanna, Heatherington & Judenko (1954) have placed such capsules which contained 1–4 g. of dimefox, close to the trunk of cocoa trees and obtained good control of cocoa mealybugs.

For smaller plants, a small charge of a systemic insecticide, for instance mipafox or dimefox, was attached to a thin wire and then coated by a substance which disintegrates on contact with moisture. The device looks much like a big matchstick and contains 0·1 g. or 0·5 g. of the systemic insecticide. It is inserted close to the plant to be protected and enables the horticulturist to market a plant which can be guaranteed for a number of weeks not to be susceptible to attack by aphids or similar sucking insects. Every watering re-distributes small quantities of the systemic insecticide charge, and thus the new foliage becomes toxic during the time that the residue is effective in the soil (Pest Control laboratory reports, 1954).

VII. RELEASE INTO IRRIGATION WATER

Where irrigation water is supplied to the field by basin irrigation it is comparatively simple to place a drum with a suitable outlet at one of the water distributors and thus let the phytopharmaceutical run into the stream of irrigation water carried to the field. While this method is attractive it has many pitfalls and will require a great deal more work before it is made foolproof; in its present stage it seems wasteful of the phytopharmaceutical, but there is clearly a great opportunity for the application of soil insecticides and certain weedkillers.

Release into irrigation water where overhead irrigation is used is effected by devices which are operated by the water flow and entrain the liquid phytopharmaceutical into the water at the dilution rate required and at the same time stop the water flow when the phytopharmaceutical is exhausted. A device is available by which the dilution is regulated by setting a valve from a maximum of 1:50 to the minimum likely to be required, controlling the quantity of phytopharmaceutical entrained into the irrigation water.

VIII. CONCLUSION

Out of the five methods of applying phytopharmaceuticals, the application of liquid dispersion has in the last fifty years emerged as the most widely used. Research work has shown in most applications that the smaller the droplets in the dispersion the better is the actual and effective cover, provided that the droplets can be deposited or maintained in the air as circumstances require. The liquid-dispersion method has therefore been developed from the application of large droplets with a M.M.D. of 250–400μ produced by hydraulic sprayers and impacted on the foliage at velocities near to the droplet's terminal velocities, to smaller dispersions with a M.M.D. of 50–100μ but applied with supporting air blast to produce a deposition velocity of the droplets which gives a satisfactory dynamic catch. Lately techniques have been developed which enter the field of true aerosols for crop protection purposes with dispersions having a M.M.D. of 10–30μ produced either by thermal or special airblast aerosol generators.

Satisfactory methods of assessing droplet sizes and deposition speeds are available but the biological evaluation of the different dispersions which the equipment available at present can achieve is lagging behind. While on theoretical grounds the ratio between effective cover and actual cover is postulated to be a maximum for a minimum droplet size, the limitations which stand in the way of further reduction in droplet size have yet to be explored.

The effective cover is often much larger than the actual cover because of short-range fumigation effects, the mobility of the insects and re-suspension of deposits in dew and rain.

Differences in dispersion at the same application rate of phytopharmaceutical per acre have a pronounced effect on the population densities of beneficial and injurious insects.

The much greater range of devices for dispersion of phytopharmaceuticals now available to the biologist calls for a deeper study of the biological effects of the various dispersion systems so that the biologist in the future will be able to write a much better specification for application methods.

REFERENCES

Akesson, N. B. & Harvey, W. A. (1948). Chemical weed control equipment. *Circ. Calif. Agric. Exp. Stn*, no. 389, 1–43.

Amsden, R. (1954). Private communication.

Bond, D. J. (1953). Trunk absorption of a systemic chemical by coffee. *Bull. ent. Res.* **44** (1), 97–9.

Brann, J. L. Jr. (1951). Mist concentrates on fruit trees. *Proc. 96th Ann. Mtg N.Y. St. Hort. Soc.*

Brann, J. L. Jr., Avens, A. W. & Dean, R. W. (1948). The application of dormant oils as mists. *J. econ. Ent.* **41** (2), 180–5.

Brooks, F. A. (1947). The drifting of poisonous dusts applied by airplanes and land rigs. *Agric. Engng*, **28** (6), 233–40.

Brown, A. W. A. (1951). *Insect Control by Chemicals.* John Wiley and Sons Inc.; Chapman and Hall Ltd.

Brown, A. W. A. (1954). Chemical control of mosquitoes in Canada. *1st Internat. Sympos. Insect Vectors Disease, Institute Superiori de Sanita, Rome.*

Brown, A. W. A. & Morrison, P. E. (1955). Studies on portable jet aerosol generators for control of adult mosquitoes. *Mosquito News*, **15** (1), in press.

Brown, A. W. A. & Mulhern, T. D. (1954). A report on tests of the performance of adulticiding machines in California. *Mosquito News*, **14**, 175–86.

Brown, A. W. A. & Watson, D. L. (1953). Studies on fine spray and aerosol machines for control of adult mosquitoes. *Mosquito News*, **13** (2), 81–95.

Cashmore, W. H. (1954). Private communication.

Castleman, R. A. (1931). *Bur. Stand. J. Res., Wash.*, **6**, 369.

Chamberlin, J. C. (1953). Characteristics of airplane spray patterns at low flight elevations with relation to insect control. *Nat. Aviat. Trades Ass. Aerial Appl. Conf.*

Courshee, R. J., Daynes, F. K. & Byass, J. B. (1954). A tree-spraying machine. N.I.A.E.

Davis, G. M. & Elliott, K. R. (1953). A rapid method for estimating aerial spray deposits. *J. econ. Ent.* **46**, 696–8.

Deonier, C. C., Sullivan, W. N., Nottingham, E. & Lindquist, A. W. (1949). Control of *Anopheles* mosquitoes with coarse and fine DDT sprays applied by airplane. *J. econ. Ent.* **42**, 447–50.

Edwards, C. J. (1953). Droplet spectra of various nozzles using 2% nigrocine in water. Unpublished Report, Pest Control Ltd.

Edwards, C. J. & Ripper, W. E. (1953). Droplet size, rates of application and the avoidance of spray drift. *Proc. Br. Weed. Cont. Conf.*

Elliott, K. R. (1952*a*). A new method of assessing aerial spray deposits. Canada Dep. Agric. Sci. Serv., Div. For. Biol., *Bimonthly Progr. Rep.* **8** (2), 1.

Elliott, K. R. (1952*b*). Organization and spray deposit assessment, Upsalquitch budworm spraying project. *Rep. Canada Dep. Agric. Div. Forest Biol.* (Mimeogr.) 71 pp.

Fraser, R. P. & Eisenklam, P. (1953). Research into the performance of atomisers for liquids. *J. imp. Coll. chem. Engng Soc.* **7**, 52–68.

French, O. C. (1942). Spraying equipment for pest control. *Bull. Univ. Calif. agric. Exp. Sta.*, no. 666.

Giess, R. W. (1953). Aerial application of granular insecticides in south eastern Pennsylvania. *Mosquito News*, **13** (2), 55–6.

Green, H. L. (1950). Problems in the atomization of liquids. *Inst. Phys. Conf.*

Gucker, T. F. & O'Konski, C. T. (1949*a*). *Chem. Rev.* **44**, 373.

Gucker, T. F. & O'Konski, C. T. (1949*b*). *J. coll. Sci.* **4**, 541.

Gunn, D. L., Graham, J. F. & others (1948). Aircraft spraying against the desert locust in Kenya, 1945. *Anti-Locust Bull.* **4**.

Gunn, D. L., Lea, H. A. F., Botha, D. H., Callaway, S., Clackson, J. R., Immelman, A., Taljaard, J. J. & Ward, J. (1948). Locust control by aircraft in Tanganyika. *Anti-Locust Res. Cent.*

Gunn, D. L., Perry, F. C. & others (1948). Behaviour of the desert locust in Kenya in relation to aircraft spraying. *Anti-Locust Bull.* **3**.

Hanna, A. D., Heatherington, W. & Judenko, E. (1954). Control of mealybug vectors of the swollen shoot virus by a systemic insecticide. *Nature, Lond.*, **169**, 334.

Hanna, A. D. & Nicol, J. (1954). Application of a systemic insecticide by trunk implantation to control a mealybug vector of the cocoa swollen shoot virus. *Nature, Lond.*, **169**, 120.

Hartley, G. S. (1952). A device for distributing liquid. B.P. 665, 655.

Hill, R. F. & Stubbs, R. B. E. (1954). The drop size spectrum of an insecticidal oil solution sprayed from an Anson XIX aircraft fitted with a rotary brush spray unit. *Porton Tech. Paper*, no. 406.

Hinze, J. O. (1948). Critical speeds and sizes of liquid globules. *Appl. Sci. Res.* A 1, 273–87.

Hoare, E. R. (1954). The development of spraying machines in this country and overseas and methods of assessing their performance. *J. Inst. Brit. Agric. Engng.* **10** (4), 3–11.

Hocking, K. S., Parr, H. C. M., Yeo, D. & Anstey, D. (1953). The application of coarse aerosols in savannah woodland containing the tsetse *Glossina morsitans* and *G. Swynnertoni*. *Bull. ent. Res.* **44** (4), 627–40.

Hocking, K. S., Parr, H. C. M., Yeo, D. & Robins, P. A. (1953). An experimental attempt to produce a fly-free corridor through a belt of tsetse-infested woodland. *Bull. ent. Res.* **44** (3), 601–9.

Hocking, K. S. & Yeo, D. (1953). Preliminary experiments in areas supporting populations of the Tsetse fly (*Glossina palpalis* (R.-D.)). *Bull. ent. Res.* **44** (3), 589–600.

Hohener, H. (1954). Weitere Erfahrungen über Möglichkeiten und Grenzen bei der Verwendung wassersparender Spritzgeräte für die Schädlingsbekämpfung im Feldbau. *Schweiz. landw. Mh.* **32** (3), 102–8.

Holmes, E. (1954). A new dusting machine. Private communication.

Hurtig, H. (1953). Development of the use of aircraft for application of insecticides and fungicides. *Agric. Inst. Review* (Ottawa), **8**, 73–4.

Hurtig, H., Mann, S. L. W., Hopewell, W. W. & Gravells, R. (1954). A new technique for sampling and assessing aerial spray deposits. *Suffield Tech. Paper* no. 51.

Husman, C. N. (1949). Spray equipment for C-47, UC-64 and L-5 airplanes. *Mosquito News*, **9** (4), 166–70.

Jeppson, L. R., Jesser, M. J. & Complin, J. O. (1952). Tree-trunk application as a possible method of using systemic insecticides on citrus. *J. econ. Ent.* **45**, 669–71.

Johnstone, H. F., Winsche, W. E. & Smith, L. W. (1949). The dispersion and deposition of aerosols. *Chem. Rev.* **44** (2), 353–71.

Jones, R. W. & Holton, J. R. (1949). Jeep exhaust venturi aerosol. *Mosquito News*, **9** (4), 161–5.

Kearns, H. G. H. (1945). Hydraulic spraying machinery for fruit crops. The choice of power equipment. *Ann. Rep. Agric. & Hort. Res. Sta., Long Ashton*, 1945, pp. 110–32.

Kearns, H. G. H. (1954). Some recent developments in the use of insecticides on field crops. *Commonw. Conf. Ent.*

Kleinschmidt, R. V. (1941). In Perry's *Chemical Engineers' Handbook*. N.Y.: McGraw-Hill.

Kruse, C. W., Hess, A. D., & Ludvik, G. F. (1949). The performance of liquid spray nozzles for aircraft insecticide application. *J. nat. Malar. Soc.* **8**, 312–34.

Laakso, J. W. & Johnson, L. H. (1949). Residue deposits on alfalfa from four types of formulations. *Bull. Mont. agric. Exp. Sta.*, no. 461, 5–15.

Lane, F. W. J. (1954). Private communication.

Lane, W. R. (1951). Shatter of drops in streams of air. *Industr. Engng Chem.* **43** (6), 1312–16.

Laplante, A. A. (1954). Concentrate spraying on deciduous fruits. Cornell University.

Lewis, H. C., Edwards, D. G., Goglia, M. J., Rice, R. I. & Smith, L. W. (1947). Atomization of liquids in high velocity gas streams. *Industr. Engng Chem.* **40** (1), 67–74.

Littage, G. (1943). *C.R. Soc. Biol., Paris*, **217**, 99, 340; 1944 *ilid.* 218, 440.

Maan, W. J. (1949). Iets over Nieuwe Typen Hefschroefvliegtuigen. *Meded. Dir. Tuinb.* **12**, 868–75.

Maan, W. J. (1951). Plantenziektenbestrijding met Behulp van Vliegtuigen. *Maandbl. Landbouw.* **8** (3), 104–12.

Maan, W. J., van Bemmel, P. M., Milborn, H. & Ten Houten, J. G. (1948). Helicopter spraying in agriculture and horticulture. *Meded. Dir. Tuinb.* **11**, 633–54.

Nicol, J. (1950). Capsid research. *W. Afr. Cocoa Res. Inst. Ann. Rep.* 1949, 50–54.

Norman, M. & Joyce, R. T. V. (1954). Private communication.

Nottage, H. B. & Boelter, L. M. K. (1942). Dynamic and thermal behaviour of water drops in evaporative cooling processes. *Trans. Amer. Soc. Heat Vent. Engrs*, **46**.

Nukiyama, S. & Tanasawa, Y. (1938–40). Physics of atomization of liquids in air. *Trans. Soc. Mech. Engng (Japan)*, **4**, 86, 138; **5**, 63, 68; **6**, 7, 18.

Payne, P. R. (1954*a*). Subsonic ramjets for helicopters. *Flight*, **66**, 737–9.

Payne, P. R. (1954*b*). Supersonic ramjets for helicopters. *Flight*, **66**, 768–9.

Pest Control Ltd. (1954). Laboratory reports.

Peterson, D. G. (1952). Thermal generated aerosols for control of biting flies in Canada. *Sci. Agric.* **32**, 289–98.

Potts, S. F. & Garman, P. (1950). Concentrated sprays for application by mist blowers for control of forest, shade and fruit tree pests. *Circ. Conn. agric. Exp. Sta.* no. 177.

Potts, S. F., Garman, P., Friend, R. B. & Spencer, R. A. (1950). Construction and operation of ground equipment for applying concentrated sprays. *Circ. Conn. Agric. Exp. Sta.* no. 178.

Potts, S. F. & Spencer, R. A. (1953). Airblast spraying apparatus for helicopters. *J. econ. Ent.* **46**, 147.

Rainey, R. C. & Sayer, H. T. (1953). Some recent developments in the use of aircraft against flying locust swarms. *Nature, Lond.*, **172**, 224–8.

Rayner, A. C. & Hurtig, H. (1952). An apparatus for producing uniform drops and its use in insecticide investigations. *Suffield Tech. Paper* no. 22.

Report on test of orchard mist spray attachment (1953). *N.I.A.E.* no. 85.

Ripper, W. E. (1938). Atomizers, a successful method for the control of agricultural pests in Central Europe. *VII Int. Ent. Congress*, pp. 3047–58.

Ripper, W. E. (1951). Selective insecticides and biological control. *J. econ. Ent.* **44**, 448–59.

Ripper, W. E. & Tudor, P. (1948). The development of a helicopter spraying machine. *Bull. ent. Res.* **39**, 1–13.

Robbins, W. W., Crafts, S., & Raynor, R. N. (1952). *Weed control*, 2nd ed. McGraw-Hill.

Rosin, P. & Rammler, E. (1933). *J. Inst. Fuel*, **7**, 29.

Ross, W. H. (1932). Granulation of fertilizers. *Ass. Off. agric. Chem.* **15** (4), 632–5.

Roth, G. A. (1954*a*). Factors affecting spray distribution from a light high-wing airplane. *3rd Ann. Texas agric. Aviat. Conf., Texas A & M College System.*

Roth, G. A. (1954*b*). Effects of wind and aircraft height on rice seed distribution. *3rd Ann. Texas agric. Aviat. Conf., Texas A & M College System.*

Sauter, J. (1926). *Forsch. Arb. IngWes.* no. 297.

Sauter, J. (1928). *Forsch. Arb. IngWes.* no. 312.

Sawyer, K. F. (1950). Aerial curtain spraying for locust control: A theoretical treatment of some of the factors involved. *Bull. ent. Res.* **41**, 439–57.

Scheubel, F. N. (1927). *Jahrbuch d. Wissenschaftlichen gesellschaft für Luftfahrt*, p. 140.

Schütz, K. (1949). Improvements relating to apparatus for distributing pulverulent or granular substances. B.P. 662, 888.

Schütz, K. (1952). Improvements in or relating to a method of and means for distributing liquids very finely. B.P. 713, 406.

Schveitger, P. H. (1937). *J. appl. Phys.* **8**, 513.

Selecting efficient equipment (1951). *Air appl. Inf. Series*, **4**.

Taylor, G. I. (1948). *Proc. 7th Int. Congr. appl. Mech.* **2** (1), 280.

TAYLOR, G. I. (1950). *Quart. J. Mech. appl. Math.* **3**, 129.

VOLTERRA, V. (1931). Variations and fluctuations of the number of individuals in animal species living together. Appendix to Chapman, R. N., *Animal Ecology*, McGraw-Hill.

VON OPPENFELD, H., BOYNTON, D., BRANN, J. L., BURRELL, A. B. & SHEPARDSON, E. S. (1952). Cost and effectiveness of different insect and disease control practices in New York apple orchards. *Bull. Cornell Univ. agric. Exp. Sta.*, no. 886.

WALTON, W. H. & PREWETT, W. C. (1949). The production of sprays and mists of uniform drop size by means of spinning disk type sprayers. *Proc. Phys. Soc. Lond.* (B), **62**, 341–50.

WEICK, F. E. (1954*a*). Tables for easy solution of common aerial applicator problems.

WEICK, F. E. (1954*b*). Notes on the design of distributors for agricultural aircraft. *3rd Ann. Texas Agric. Aviat. Conf., Texas A & M College System.*

WEICK, F. E. (1954*c*). Aircraft spraying and dusting. *Agric. & Fd Chem.* **2** (11), 546–52.

WEICK, F. E. & ROTH, G. A. (1954). Recommended nozzle locations for optimum patterns. *3rd Ann. Texas agric. Aviat. Conf., Texas A & M College System.*

WHITEHEAD, F. E. (1953). Improving aerial applicators. *Mosquito News*, **13** (2), 56.

WILSON, C. S. (1950). Aerosol spray units for control of biting insects. *Mosquito News*, **10** (2), 51–4.

WILSON, C. S. (1951). Control of Alaskan biting insects in Public Health problems in Alaska. *Publ. Hth Rep.* **66** (29), 911–44.

WILSON, H. F. & JANES, R. L. (1942). Electrostatic charges of inorganic and organic dusts. *Soap, N.Y.*, **18** (3), 93–5; **18** (4), 103–5.

WOOTTEN, N. W. & SAWYER, K. F. (1954). The pick-up of spray droplets by flying locust. *Bull. ent. Res.* **45**, 177–97.

YEO, D. & THOMPSON, B. W. (1954). The deposition in open country of a coarse aerosol released from an aircraft. *Bull. ent. Res.* **45** (1), 79–92.

YEOMANS, A. H. (1949). Directions for determining particle size of aerosols and fine sprays. *USDA Bur. Ent. & PQ., ET–267.*

YEOMANS, A. H., ROGERS, E. & BALL, W. H. (1949). Behaviour of aerosol droplets. *J. econ. Ent.* **42**, 592–6.

EXPLANATIONS OF PLATES 7 AND 8

PLATE 7

Fig. 1. A giant hydraulic sprayer for citrus; the output of a multi-stage centrifugal pump is discharged through cyclic oscillating guns; designed by Dr Carman of the University of California Citrus Experiment Station.

Fig. 2. A new experimental agricultural aeroplane, hydraulic sprayer; tank in front of pilot; special gull wing for good visibility; shown spraying orchards.

Fig. 3. Agricultural aircraft specially designed for treatment of crops, shown dropping fertilizer. External corrosion-resisting finish; tricycle undercarriage; engine cooled by ejectors operated by exhaust, seen in front of the mainplane.

Fig. 4. A mist blower designed by Dr Brann of the Department of Entomology, Cornell University; the outlets rotate and for crop spraying the discharge unit is directed fore and aft.

PLATE 8

Fig. 1. A portable thermal aerosol generator; the insecticide is injected into the exhaust of a pulse jet.

Fig. 2. A shoulder and chest-mounted mist blower intended for plantations and difficult terrain on which wheeled equipment cannot operate; the power unit is in the fan on the back, while the tank for the spray chemical is carried at the front.

Fig. 3. A soil applicator for spot treatment, an auxiliary unit for mounting on a conventional hop sprayer, which discharges a measured dose to each hop plant, actuated by a breaker bar which operates a flap valve.

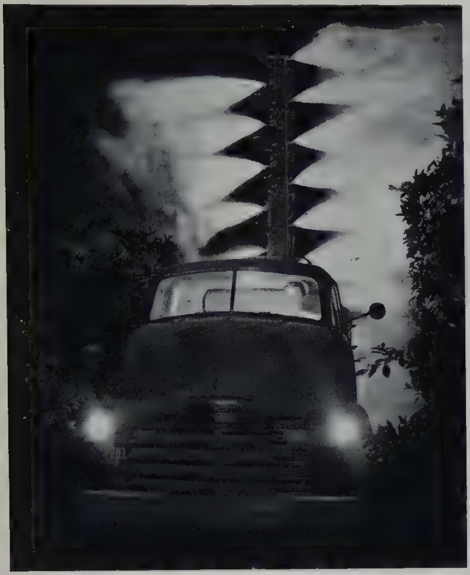


Fig. 1

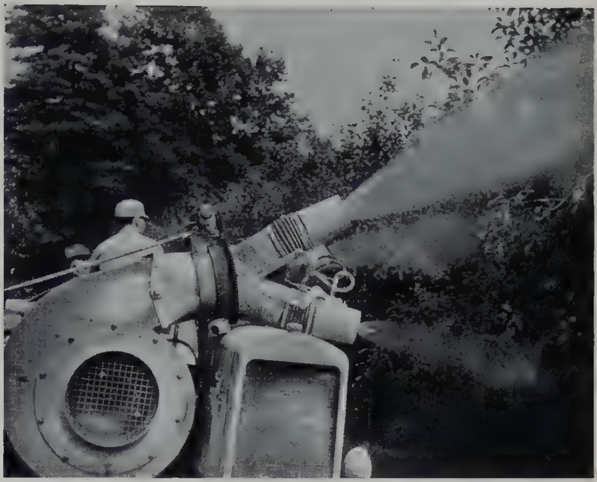


Fig. 4

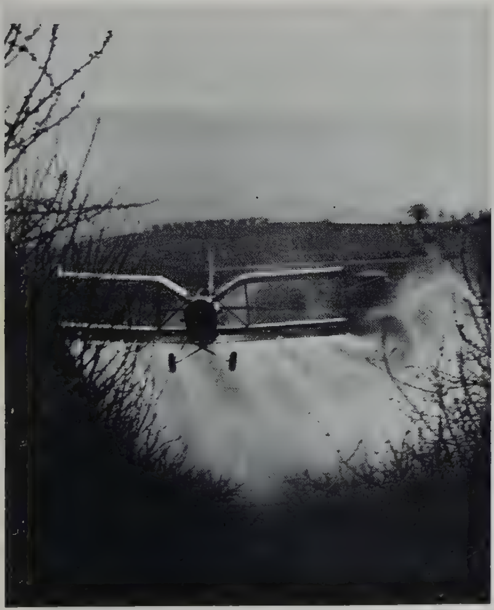


Fig. 2

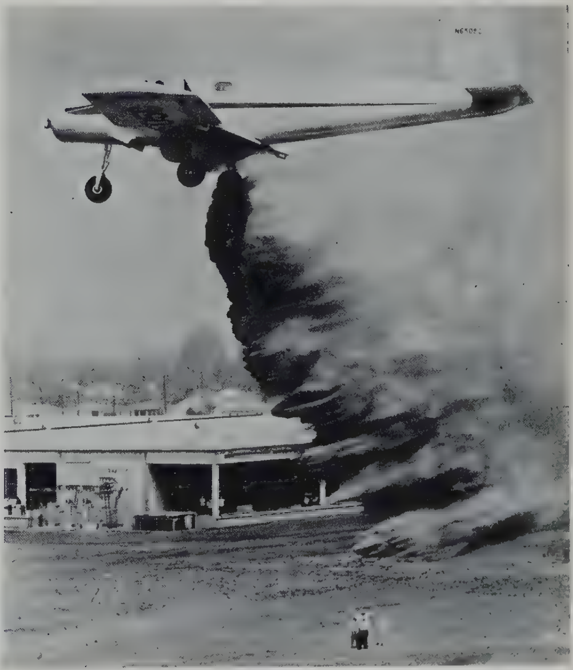


Fig. 3

RIPPER—*Application methods for crop protection chemicals*

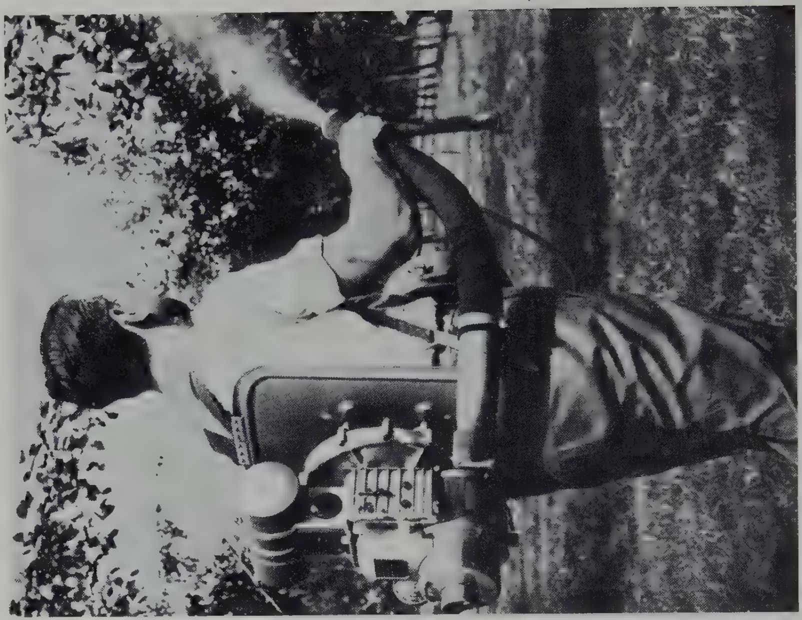


Fig. 2

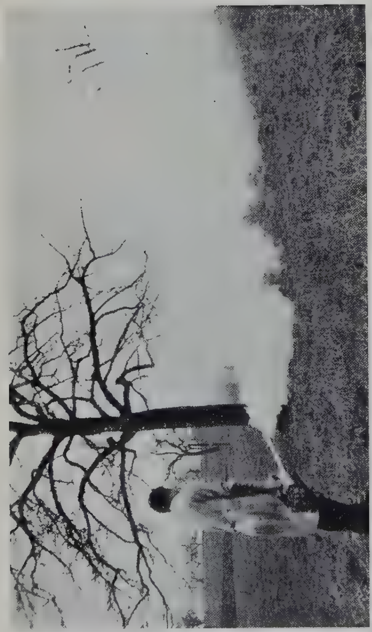


Fig. 1

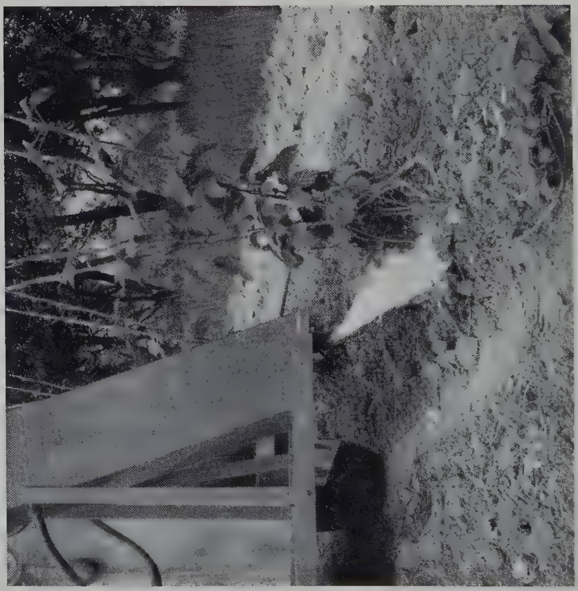


Fig. 3

RIPPER—*Application methods for crop protection chemicals*

Holmes, E. (1955). *Ann. appl. Biol.* **42**, 325–332

THE CONTRIBUTION OF COMMERCE TO CROP PROTECTION

By E. HOLMES

Head of Technical Department, Plant Protection Ltd, Fernhurst Research Station, Haslemere, Surrey

The last time I was privileged to address members of the Association of Applied Biologists all the official speakers and all speakers in the subsequent discussions were agreed that measures for crop protection are needed if full advantage is to be taken of the world's immense efforts in crop production. We were not so much agreed regarding the exact methods of crop protection to be employed in particular circumstances. Nevertheless, there was almost universal agreement that, despite some misuse of chemicals in the past and some unfortunate and costly results of that misuse, in the present state of knowledge the intelligent use of crop protection chemicals is absolutely necessary if we are to harvest and store safely the world's production of food and other crops.

In speaking of the contribution of commerce—and I assume this means industry and commerce—in this field I shall, for obvious reasons, deal mainly with chemical contributions. I hope, however, to be able to demonstrate that even the chemical companies primarily interested in this work have also made valuable additions to our knowledge in related spheres.

PUBLIC RELATIONS

I have recently been re-reading with delight chapter 24 of Large's book *The Advance of the Fungi* entitled 'Calling the Chemical Industry'. In this he draws attention to '...a most interesting game of devils and angels. The very enterprising but at best commercially-honest spray-manufacturers played the darker part; while the much less enterprising but impeccably veracious professors and lecturers in the University Departments flapped their indignant wings in pure white light'. That was 30 or 40 years ago!

The position is very different to-day. With very few exceptions there are excellent relations between the official bodies and workers at research stations and universities on the one hand, and industry on the other. It has come to be recognized that many commercial firms are doing serious research work and making worth-while contributions to the common problems. To ride one of my own hobby horses for the moment, I would say yet again that official workers and research stations often know considerably more about local agricultural and biological problems than we in industry, whilst we, on the other hand, have access to many more entirely new types of chemical. The more we learn to trust each other and to work together, the quicker we shall jointly solve growers' problems and arrive at agreed measures to improve world crop protection and therefore world crop production.

I personally have been very glad to have been associated with the change that has taken place in the last 25 years or so and to say that we on the industrial side are happy that the barriers have been broken down.

One other general point; from time to time we are accused of stealing good technical men from the universities and research stations, and it is true that, like every other institution, we attempt to recruit the best staff we can from wherever they may be working. On the other hand, I would draw your attention to the fact that occasionally we make contributions in the opposite direction! S. J. Watson who was in charge of Jealott's Hill at the time of the discovery of MCPA and 2 : 4-D is now Prof. Watson at Edinburgh. G. E. Blackman also did a lot of his early work at Jealott's Hill and is now Prof. Blackman at Oxford. Others of your members, J. R. Busvine and J. D. Fryer, worked at Hawthorndale and Fernhurst some years before proceeding to the London School of Hygiene and Tropical Medicine and Oxford, respectively.

With these few introductory remarks I propose to treat my material under the heads:

(1) Fundamental biological and chemical studies.
(2) Work on new chemicals.
(3) Work on techniques.
(4) Costs of development of new chemicals.
(5) Economic benefits to agriculture.

FUNDAMENTAL BIOLOGICAL AND CHEMICAL STUDIES

Despite what I have just said a very considerable amount of fundamental biological research work, usually associated with chemical work, goes on in some of the larger commercial organizations. It would be quite impossible here to do more than give a few examples of this sort of thing; I propose to draw upon our own experience even for these examples.

Back in 1939 Ferguson, then in the research department of the General Chemicals Division of I.C.I., published the results of some most interesting work on the relationship between biological activity and variations in the values of certain physical constants in homologous series of chemicals. He showed that the toxic concentrations of individual chemicals in homologous series to various organisms follow quite closely many of the physical constants of the series. Where the curve of biological activity showed a maximum he was able to demonstrate that some other physical factor was coming into play to neutralize the original factors.

I need hardly draw the attention of an audience such as this to the rather remarkable work of another colleague of mine, P. W. Brian, working at the Frythe, Welwyn.

His publications on the subject of antibiotics and the indications from his work that advances in this field may well lead to advances in crop protection speak for themselves. Although he himself would agree that he has not yet produced anything justifying commercial development, I am very hopeful that products of worthwhile interest to agriculturists will eventually emerge.

Similarly, it will be within the knowledge of many present that Templeman's early work into the fundamental effects of plant growth regulators on the growth of crop plants, carried out in the years just prior to the last war, eventually led to the discovery by Slade, Sexton & Templeman (1945) of the plant growth regulator type of selective weedkiller. This has led to tremendous practical developments. The work of the team at Jealott's Hill continues, and I feel quite sure that any farmer looking round those laboratories at the present time would have some difficulty in believing that the Langmuir trough used by R. C. Brian, and other techniques, could conceivably have any relationship with farm practice of the future.

Work on new chemicals

Whilst discussing the draft of this paper with a colleague a few days ago he pointed out that I had left out the most important single contribution of industry, namely, that it makes chemicals! May I put the point in another way. From time to time when young graduates come on to our staff it is obvious that they are not quite sure whether it is entirely respectable for scientific men to join a commercial company. It is amusing to see the change in their attitude when the realization comes that all the biological and chemical research work in the world is of no use to the farmer unless somebody actually makes the basic chemicals and formulates the products for use on crops.

A short time ago colleagues of mine at Fernhurst produced a list of most of the new crop protection chemicals—insecticides, fungicides and weedkillers—which have appeared in world literature and been used to a greater or lesser extent in agricultural practice in the last 15 years or so. It is not surprising that, without exception, they come from countries with well-established chemical industries. In fact, of a total of 78 listed, 55 came from the United States, 8 from Germany, 7 from the United Kingdom, 7 from Switzerland and 1 from France. This sounds like a very considerable preponderance of effort and result in the United States, but when fundamental discovery rather than follow-up work is considered, the picture is rather different.

I now propose to pick out those discoveries and developments, including developments by commercial companies of leads produced by individuals or official bodies, which have already made a considerable impact on practical agriculture in many parts of the world.

Insecticides

Taking insecticides first, obviously the era started with the discovery of DDT by Geigy in Switzerland. This was followed by the discovery in France by Dupire and Raucourt that the mixed isomers of benzene hexachloride had marked insecticidal properties. I think, however, we can claim that the demonstration that gamma-BHC was the active portion of the mixture, and the main early development of gamma-BHC, go to the credit of I.C.I. and P.P. in Britain.

Following these discoveries many firms proceeded to chlorinate many hydrocarbons and other chemicals and, as a result, we had toxaphene from the Hercules Powder Co. in the United States and a little later the aldrin/dieldrin group of insecticides, first from the Velsicol Corporation, later from Julius Hyman and Co. and now, of course, from Shell Chemicals, originally in the United States.

During the same period the old I.G. and, later, Farbenfabriken Bayer in Germany developed the phosphorus esters and in particular TEPP, parathion, schradan, demeton and now a modification of demeton under the trade name, 'Meta-Systox'. Arising out of these discoveries Pest Control Ltd. and others in Britain have done much development work on schradan and produced new compounds of similar or related types. Similar work has been done by the American Cyanamid Co. and others in the United States.

During the same period again a large number of acaricides, other than the phosphorus compounds, have been discovered and, to pick a single example, the Dow Company in the United States produced PCPPCBS which is now being used commercially to a considerable extent as an ovicide, not only in the United States but in Britain and elsewhere.

Fungicides

Before dealing with recent developments in the fungicide field I would like to digress and mention the development in the first decades of this century of the mercurial seed dressings. Within the last 2 months I have been interested to visit Chemische Fabrik Marktredwitz in Bavaria (the oldest chemical factory in Germany) and to realize again that they produced their first inorganic mercury seed dressing in 1909 and their first organo-mercurial, following the work of Hiltner, in 1913. (I should add that this is one year before the first reference given by Large and Martin in their books, and in our own exhibit at this Jubilee Conference!) I mention seed dressings because, apart from the discovery of Bordeaux and Burgundy mixtures and the development of sulphur fungicides, the organo-mercury seed dressings have probably had more influence on the control of fungus diseases in agriculture than any other chemicals. They are also the basis of considerable developments in the technique of using both fungicides and insecticides at the present day.

In the past 15 years or so we have seen the considerable development of the organic sulphur fungicides (the 'educated' sulphurs with the Old Testament names)

—first thiram by the I.G. in Germany and ourselves in Britain, and later ziram and ferbam by du Pont and zineb and nabam by Rohm & Haas, both in the United States.

Another outstanding development has been that of captan (SR.406) by the Esso Company in the United States.

Weedkillers

Turning to weedkillers, there is no doubt that the most outstanding discovery was that of MCPA and 2 : 4-D which Templeman described to you in detail yesterday, followed by 2 : 4 : 5-T in the United States and IPC, again by Sexton & Templeman in this country.

Other potentially important discoveries, not yet fully evaluated, are those of TCA and CMU, etc. by du Pont, and subsequently dalapon by Dow in the United States.

I am well aware that in making this somewhat arbitrary selection I am leaving myself open to the charge that I have omitted other important discoveries; I would remind you that I did start by saying that I proposed to list mostly those developments which, in my opinion, had already made a considerable impact on world agriculture.

From the list I have just given it is evident that, despite the figures at the beginning of this section, we in Britain have certainly contributed at least our share of the more important new discoveries in the last decade and a half. If I had to guess at the discoveries with the greatest practical importance so far, I would say that DDT, gamma-BHC and the growth regulator weedkillers would easily head the list—and two of these have come from Britain.

WORK ON TECHNIQUES

Under the heading of techniques I originally proposed to refer to our own development of combined cereal seed treatments for the simultaneous control of deleterious fungi and insects as a new technique. It was pointed out to me quite forcibly by my colleagues, that there is nothing new under the sun and that the treatment of onion seed with an insecticide is quite an old procedure.

However, I well remember the original discussions at the Hawthorndale Laboratories, back about 1944, regarding the theoretical possibility of incorporating the newly discovered gamma-BHC in organo-mercury seed dressings with the idea of protecting cereal seedlings from the ravages of wireworm. Most of us considered that the application of 1 or 2 oz. of gamma-BHC in this way could scarcely have any appreciable effect on the wireworm population of the thousand tons or so of top soil per acre. Nevertheless, the experimental work proceeded and to our surprise very successful results were obtained (Jameson, Thomas & Tanner, 1951). Not only has this technique gone a long way towards safeguarding cereal crops in this country, but it is being developed very extensively in North America for the same purpose, in South Africa for the prevention of black beetle on maize and in certain tropical and subtropical areas for reducing the depredations of termites and other soil-inhabiting insects. It has also reduced the cost of such measures to a remarkable degree.

A newer technique of a totally different kind has been the introduction of low-volume methods of spraying crop protection products. I personally was associated during the war years, 1942–5, with the development of the first practical air-blast low-volume sprayer in this country—originally for spraying potatoes against blight and Colorado beetle, but subsequently for the application of selective weedkillers. The particular machine developed is very effective technically but rather expensive.

In 1947 Templeman brought back to this country from the United States the idea of the hydraulic low-volume sprayer and, starting with two experimental machines in 1948, I am assured that something like 20,000 have been sold in Britain alone to date. By reducing the amount of water required per acre and using a relatively simple machine, the whole costs of spraying have been enormously reduced and spraying has been brought within the means of a tremendous number of farmers who never contemplated such operations in the past.

I am afraid I have rather strayed on to the field of Dr Ripper who has just been talking about the development of application methods, but I did want to make the point that, in this country at least, these new developments have come primarily from commercial firms.

COSTS OF DEVELOPMENT OF NEW CHEMICALS

Before dealing with the economic benefits from using crop-protection chemicals, I think it worth while directing your attention once more to the very considerable cost of developing entirely new chemicals in this field. Many of you will have seen the original paper on this subject by Wellman in 1952. Some of you may have heard me quote that paper to the effect that, even when laboratory tests and small- and large-scale field trials cost only a few hundred pounds per chemical tested, the consolidated cost of the development of an entirely new 'break' can be as much as half a million pounds sterling. Earlier this year I had the pleasure of meeting Wellman of the Carbide and Carbon Chemical Corporation at the Boyce Thompson Institute, Yonkers, New York; he told me that his paper had created very considerable interest, and that visitors and correspondents had either confirmed his estimates or indicated that they were on the conservative side.

I do suggest to an audience such as this that factors of this kind should be borne in mind when discussions take place on costs of crop-protection products. I would also draw attention to the fact that if a crop-protection product is really efficient for the purpose in hand, the person who gets most profit is the user rather than the manufacturer. May I give one or two examples?

The Department of Agriculture, Uganda, has shown that the use of seed dressings on cotton seed to control the blackarm organism, on some 82,000 acres in 1950–1, resulted in a crop increase worth something of the order of half a million pounds. This was the result of the use of a product costing about £2000 on which the manufacturer could not possibly have made more than a few hundreds profit (Tipler, 1952). When it is considered that cotton represents some 75% of the total exports of Uganda, it is not surprising that His Excellency the Governor of Uganda pronounced this work to be one of the most important agricultural developments taking place in the British colonies.

Again, in the use of combined insecticide/fungicide seed dressings in this country, costing anything from 4*s*. to 10*s*. per acre, the benefit to the grower can easily be of the order of £5 to £10.

Economic benefits to agriculture

Losses due to pests will be discussed in several papers this afternoon and were admirably indicated in Ordish's recent book *Untaken Harvest*. The benefits derived by agriculturists from the use of crop-protection products have been the subject of very considerable investigation all over the world. My own colleagues and other workers in official and commercial organizations in this country are also intensely interested. The data available are not very precise, but in the following sections I shall hope to demonstrate that certain of the contributions, in this country at least, are very significant.

The most important limiting factor in cereal production in Britain is almost certainly weeds. It has recently been estimated that out of a total area of cereals of approximately 8 million acres, something between 2½ and 3 million acres are treated each year, mainly with the growth-regulator type of weedkiller but to a smaller extent with DNC. Accepting Templeman's average figure for the resulting increase in yield as 3 cwt. per acre, which is more conservative than Blackman's, this represents an increased yield of the order of 400,000 tons of grain.

The next most important causes of loss are the seed-borne fungus diseases of cereals and here it is estimated that something over 80% of the seed sown is treated with organo-mercury fungicidal seed dressings. We consider the average loss due to these organisms as 6–7% in crops from untreated seed, or a gain of about 1 cwt. per acre in treated crops. On the acreage figures just given this represents an increased grain yield of well over 300,000 tons per annum.

Probably the third most important cause of loss is wireworm. This is obviously much more sporadic in its attack and much more important on the average in the south-east than in the north-west, but assuming a loss in untreated crops of the order of 20% on 20% of the total acreage concerned, i.e. 4%, and an acreage treated last year of over 500,000, then the increased grain yield was of the order of 90,000 tons. The acreage being treated in the current season is much higher.

Turning to the potato crop, the main pest causing loss is obviously blight, and here we have a fair amount of reliable evidence showing that losses are of the order of 10% in the field and 2 or 3% in store. Both of these may be prevented by timely treatment with copper sprays or dusts. Of the total area of potatoes of nearly one million, probably a quarter should be worth spraying most years, although considerably less than this is normally treated. Estimating that only about 70,000 acres are treated with copper at the present time, then the gain to the country is of the order of 60,000 tons of potatoes.

Sugar beet, of course, is an important crop grown on some 400,000 acres, and the whole of the seed for this area is at present treated with organo-mercurial seed dressings. These are estimated to prevent losses of the order of 6–8%, giving an increased yield of the order of 13 cwt. per acre or over a quarter of a million tons of beet per annum throughout the country.

Less reliable figures can be found for many other crops, but I have probably given sufficient examples to indicate that crop-protection measures using chemicals now available from industry are making worth-while contributions to the national agricultural effort. At the same time, there is no doubt that in many instances these measures could be increased with correspondingly greater increased returns.

In conclusion may I say that, together, official workers and workers from industry have developed crop protection out of all recognition in the past fifteen years. I hope I have been able to show that, starting from what some folk regarded as rather disreputable beginnings, industry has grown respectable and is now taking a full share in these developments.

REFERENCES

FERGUSON, J. (1939). *Proc. Roy. Soc.* B, **127**, 387.

HILTNER, L. (1915). *Prak. Bl. PflBau*, **13**, 65.

JAMESON, H. R., THOMAS, F. J. D. & TANNER, C. C. (1951). *Ann. appl. Biol.* **38**, 1.

SLADE, R. E., SEXTON, W. A. & TEMPLEMAN, W. G. (1945). *Nature, Lond.*, **155**, 498.

TIPLER, R. V. (1952). *Contr. IIIrd Int. Crop Protection Congress.* Paris.

WELLMAN, R. H. (1952). *Agric. Chemic.* **7**, 32–34.

Forecasting and assessment of plant diseases

Chester, K. Starr (1955). *Ann. appl. Biol.* **42**, 335–343

SCIENTIFIC AND ECONOMIC ASPECTS OF PLANT-DISEASE-LOSS APPRAISAL

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As we celebrate the completion of the first fifty years of the Association of Applied Biologists and look forward to the next fifty, we are well aware of the greatest biological problem facing the world to-day, that of the rising tide of humanity. Already half the world is underfed or starving. As applied biologists, we are striving to whip this problem on many fronts, by increasing the capacity of land to produce, by fuller utilization of the products of the soil, and by development of new and unconventional food supplies.

A major opportunity for bringing food into better balance with population is in eliminating preventable losses in agricultural commodities such as are caused by fungi, bacteria, viruses, nematodes, insects and mites, rodents and weeds. We might even consider the 'losses' resulting from the inefficiency of normal plants and animals, since we are learning that with chemical or physical stimulation, the productivity of plants and animals can be increased beyond levels that have been considered normal. While the subject of this paper is limited to the losses caused by plant diseases, I must ask your indulgence if, at times, I range somewhat more broadly in the field of agricultural losses.

What is the magnitude of these losses in our agricultural production? The latest estimates from the United States Department of Agriculture, covering the decade 1942–51, indicate that in the United States nearly one-third is lost from the potential value of crops, livestock, and forest products. This loss equals the production of five hundred million acres of crop, pasture, range and forest land. One-tenth of potential farm production in the United States is believed to be sacrificed to plant disease and another tenth to insects. These estimates are probably too low because of our failure to attach significance to losses that are not spectacular.

These staggering losses are in the United States where agricultural science has reached a relatively high level. How much greater may the losses be in those countries that have not advanced as far, technologically. To most people, even to many scientists and farmers, only the dramatic attacks on our farms are recognized: the recurrent plagues of locusts and epidemics of grain rusts since Bible times, the holy fire of the Middle Ages that we now recognize as ergot, the potato murrain of a century ago, and the chestnut blight and oak wilt of more recent times. More destructive are the losses that are less obvious but always with us, unrecognized or overlooked because they are so common that affected crops or livestock are thought to be normal.

We are inclined, too, to interpret agricultural losses only as they affect the farmer, whose economy, after all, is adjusted to absorb rather well this constant drain upon his production. We tend to overlook the effects of these losses on our society as a whole. Farm commodities have inelastic statistical demand curves, such that, in a free market, the farm income from moderately decreased production tends to be greater than that for moderately higher production. It is the industries that depend on agriculture, and above all the consumer, that have an even greater stake in farm loss prevention than does the farmer. Whatever the losses in agriculture, it is the consumer that must absorb them in higher prices, lower quality, and taxes to permit the farmer to operate despite agricultural hazards.

Reasonably extensive and accurate information on the nature and amount of the various losses suffered by agriculture can be an extremely useful thing. Our resources for agricultural research, education and regulatory activities are restricted. We must know the true proportions of each agricultural hazard so that our limited efforts and funds are directed at those which are most injurious to the economy.

There are other important uses for such information. It is needed by the industries that serve agriculture, for example, to indicate potential markets to the manufacturers of pesticides. It is needed in such activities as planning land utilization, appraising the value of land, calculating crop insurance rates, and determining the probability of success or failure of new agricultural ventures. In this last connexion, we recall that one of the major factors in the failure of the East African groundnut scheme was a lack of recognition of the potential and, as it proved, actual destructiveness of the rosette disease.

Those of us who serve agriculture have a more subjective interest in having reasonably accurate information on agricultural losses. Whether we like it or not, it is a fact that support for our work, be it research, education, or regulation, is directly related to the national economy and must be justified in terms of our contributions to that economy. Those who control the purse strings, on which our work depends, must be made to realize the magnitude of the losses that we are striving to overcome. Guesses are not enough; we must be able to prove the economic significance of our work.

Incidentally, in a number of our scientific fields we have done a rather poor job of public relations. The significance of our work is not at all apparent to many who should recognize it. In the United States, at the moment, this is strikingly brought out by the wide publicity being given to the toxicological hazards of agricultural chemicals, contrasted with a relative failure to make the public aware that such chemicals are indispensable to maintaining and increasing farm production and, if properly used, are quite harmless to man. For the value of our work to be recognized, however, we again must have facts on the losses which we are striving to overcome.

In striking contrast to our need for these facts is our appalling lack of them. Too often we are in the position of a police department that does not know which acts of misconduct are misdemeanours and which are felonies, or that of a life insurance company that does not know the relative significance of the various causes of death. I could mention numerous cases in which it has been proven that what we thought were competent estimates of plant-disease losses have been in error by as much as 1000%.

There is, for example, the case of the disease of potato caused by the agent variously known as the X virus, the latent potato-mosaic virus, or the 'healthy potato virus'. Discovered in 1925, this virus has been present in practically every potato plant grown in America, except new seedlings. Not for 20 years was its damage measured and found to average 13% of the crop, a figure confirmed by independent loss measurements in America, Australia, Scotland and England. This measured amount of loss from latent mosaic is twice as great as the average annual loss in the United States from potato late blight, *Rhizoctonia*, and scab combined, and 4 times the annual average loss from late blight, according to our best official estimates of losses from these other diseases. Applying this figure, 13% loss, to American potato production, during those 20 years latent mosaic caused a total loss of more than one billion bushels of potatoes. The bases for control of this disease by seed certification and varietal resistance were available at the time. If the damage from latent mosaic had been measured and recognized when the disease was first discovered, if research on its control had been immediately undertaken, and if no more than one-tenth of this loss had been averted as a result, the gain would have amounted to 110 million bushels of potatoes with a value dwarfing to insignificance the cost of the research involved.

Widely scattered experiments on insecticidal spraying of lucerne, in the absence of any known important insect pest, have doubled or even trebled the yields. Obviously, what has been regarded as normal lucerne production has fallen short of potential production by one-half to two-thirds owing to the damage caused by insects that have been regarded as harmless. We are just now learning that the situation is similar as regards some of the lesser-known soil nematodes and root-feeding fungi. We are coming to the opinion that some of these nematodes, which have been little more than taxonomic curiosities, are actually more destructive than the root-knot nematode on which so much of our efforts at control have been expended. It is similar with the root diseases of cereals.

Simple observation can be most deceiving. Before making measurements, I had supposed that the amount of leaf rust present in Oklahoma wheat fields on 1 April probably did not vary from year to year over a range broader than one to one hundred. Measurements during 10 years showed that this range actually extends from one to one million.

The defects in plant-disease-loss appraisal in the United States are illustrated in publications of the United States Department of Agriculture where total losses from cotton diseases are stated as 0·8% in 1948 and 1·1% in 1949 compared with 17·5% loss attributed to one insect species, the boll weevil, in 1949. Those who have worked on cotton diseases know that the losses are nearer 10–20% annually. In

Texas alone, the loss from Texas root rot has been reliably calculated at $100 million per year. This gross underestimation of cotton diseases, which influences research allocations, was called to the attention of the Secretary of Agriculture.

Our comparative ignorance of plant-disease losses is understandable in the light of the evolution of plant pathology during the past fifty years. In 1904, Blackman in England and Blakeslee in the United States were making the first exciting discoveries of the mysteries of sex in fungi. Then, plant pathology was largely mycology, with emphasis on taxonomy. Pathogen plus host equalled disease; it was as simple as that. As the science evolved, it passed through phases of stress on the physiology and ecology of plant disease and the biology of pathogens. It was dismaying to me to sample through the journal, *Phytopathology*, over the years, and find so very little attention given to the economic significance of plant disease. In extensive and otherwise complete monographs on given diseases, the subject of economic importance has often been dismissed in a sentence or a phrase.

Erroneous loss estimates can be very harmful. If they are too low, it leads us to neglect the loss factor, and if they are too high we misappropriate effort which should be spent on more important problems. It is a step forward that we recognize that many of the estimates which have appeared in print, are of very doubtful accuracy. By definition, an estimate is a judgement or opinion, usually implying careful consideration or research, a judgement made by calculation, especially from incomplete data. On this basis, many of the figures which we call estimates should more properly be called guesses. In the States, we sometimes refer to them as 'guesstimates'. One sometimes hears criticisms of estimates as though they had no place in the activities of accuracy-loving scientists. But as properly defined, with their limitations recognized, they may often be of value to us provided we know their probable range of accuracy.

Among the many problems in loss estimation is the fact that agricultural losses are often very complex, including both quantitative and qualitative elements and indirect or collateral features. Most published loss estimates are simply quantitative, in terms of production units: tons, or bushels, or bales. Yet, losses in quality may be even more important. As one of many examples that might be cited, recent work in the southern United States has shown that while the anthracnose disease does not appreciably affect the amount of yield of Sudan grass, it reduces the content of fat and protein by 9% and increases the lignin by as much as 20%. The digestibility of the grass is much reduced, and the loss is almost entirely qualitative. In our estimates of loss, we should strive to include all forms of loss from planting of the crop to its final disposition. Ideally, this includes such indirect losses as the decrease in activity, economical operation, and profits of those industries that are dependent on agriculture such as grain elevators, mills, processing plants, railroads, banks, and the industries that furnish farm supplies.

This is not the time and place to undertake a detailed discussion of the methods of loss appraisal. An extended exposition of these is given in a monograph that appeared as a supplement to the *Plant Disease Reporter* in 1950. Here my remarks must be confined to certain general principles applying to the problem of loss appraisal.

The objective of plant-disease-loss appraisal is threefold: to determine the amount of disease, which is the product of its prevalence and its intensity in individual plants; to translate the amount of disease into loss, expressed as percentage of potential, disease-free crop, or in production units; and to interpret the effects of this loss on the economy. It is recognized that the last of these, the interpretation of the effects of loss, is a problem for economists and sociologists and lies outside the domain of our experimental science. Nevertheless, it is a very necessary part of the loss problem.

The methods used in plant-disease-loss appraisal must meet certain standards. They must be comparable, so that the results obtained by any worker in any location and in any season may be integrated with those obtained by other workers or in other seasons and locations. The methods must be objective; the serious errors that result when estimates are coloured by personal opinions have already been pointed out. In so far as possible, appraisal should include all forms of loss, quantitative and qualitative, direct and indirect. Consideration must be given to the various factors that can influence the degree of loss, including the variety of a crop, the physiologic strain of pathogen involved, the stage of development of the plant at the time of disease attack, the tempo of disease development, the intensifying or ameliorating effects of the various environmental factors, and the combined effects of two or more loss factors acting concurrently.

The degree of desired accuracy in loss appraising must be a compromise. It must be sufficiently high that the results are useful and have meaning, but it can never approach the level of accuracy obtained in critical laboratory experiments. Perhaps an error no greater than ± 10% would be a reasonable target.

It would be useful to have two categories of appraisal methods. One would serve the purposes of the scientist who wishes to examine the effects of plant disease in considerable detail and with a rather high degree of accuracy. The other class of appraisal methods would be simpler, somewhat less accurate, rapid, and suited for use of crop scouts and inspectors who have neither training in nor need for highly detailed analyses of the effects of disease but who do need to know the order of magnitude of disease losses.

The techniques for determining the prevalence and intensity of plant diseases are covered in detail in the monograph to which I referred. They may involve counting diseased plants or organs or estimating the volumes of plant tissues affected, which is frequently assisted by the use of printed scales depicting series of degrees of plant attack.

In surveying, to determine the destructiveness of disease over a wide land area, guiding principles have also been developed, among them the desiderata in sampling degrees and methods.

There are many techniques that may be used in converting amounts of disease into amounts of loss. Each has its advantages and its limitations. These are described in the monograph that has been mentioned and I will not discuss them further except to point out that sound principles of the methodology have been worked out and a good beginning has been made toward providing us with methods that are suitable for the task of disease-loss appraisal that lies before us.

As we gain more information on the economic significance of agricultural losses, the question arises as to the best use of such information. We have already considered the need for this information, to guide research, educational, and regulatory programmes, to assist the industries that serve or depend on agriculture and the economists who assemble and interpret agricultural statistics, to assist in the planning of land utilization and new agricultural ventures, and to justify expenditures for agricultural science. It follows that the results of loss appraisal must be brought to the attention of the men who are responsible for such activities as these. The economic impact of agricultural losses must also be made known to the housewives, wage-earners, businessmen and legislators. While full details of this work must be placed on permanent record in our technical journals, the importance of public relations in this connexion should not be forgotten, and our findings should ultimately find their way to the layman in non-technical language through each of the media of public information.

I hope that I have not created the impression that little is currently being accomplished in the appraisal of agricultural losses. On the contrary, there is every evidence of growing interest and activity in this important phase of our work. The modern science of plant-disease-loss appraisal is only 25 years old if we date it from the first comprehensive work on the subject, Yachevski's *Guide to Phytopathological Observations*, published in 1929. In this short time, and especially during the past 5 years, much interest has been aroused in many countries in plant disease surveying, in research to devise better methods for disease and loss appraisal, and in the publication of loss information. Indeed, the fact that a session of this conference is devoted to this subject is indicative of the rising interest in plant disease forecasting and assessment.

It is appropriate that such a session, the first of its kind, should be held in England, since England is leading the field to-day in its scientific approach to this problem. I know of no other country where men are wholly engaged in studies of plant disease and insect appraisal as are Large and Strickland. The rest of the world is indebted to England for its pioneering in the preparation of scales and directions to aid in surveying for diseases such as those of grain and potatoes, and for the numerous publications in this field that are constantly appearing, such as those of Beaumont and Large on potato disease assessment, or those of Croxall and his associates on apple scab. These workers are particularly to be commended for including consideration of the growth stages of plants in relation to the destructiveness of diseases, and for devising scales for estimating growth stages.

Elsewhere in the world, the current interest in research on methods for disease appraisal is seen in the work of Gram and his associates in Denmark, of Greaney who has contributed so much to our understanding of disease losses in cereal crops, of certain Russian workers following the pioneering efforts of Yachevski and Vavilov, of Palti in Palestine, Vasudeva in India, Tehon in the United States, and others who might equally be mentioned.

As a further indication of interest in this subject, there was organized in 1952 an International Commission on Plant Disease Losses, functioning in the International Union of Biological Sciences, co-operative with UNESCO. This Commission is concerned primarily with methods of loss appraisal, leaving the dissemination of loss information to other agencies. Until this year, the activity of the Commission was confined to exchange of information by correspondence, but last July opportunity was afforded for a meeting of the Commission, in connexion with the Botanical Congress in Paris, under the chairmanship of Dr Gram.

In addition to these efforts toward improved surveying methods, plant disease surveying itself is on the increase. Again we have an excellent example in England in the work of the National Agricultural Advisory Service. Denmark has also pioneered in this field, with a wholesome influence on other countries; for example, the plant disease surveying in Holland under Dr Briejer is modelled after the Danish programme. Plant disease surveying in the Netherlands is noteworthy from the standpoint of some of the unusual techniques that are being successfully used. I think in particular of the very intensive nematode survey, the laboratory in Wageningen reminding me of a factory-production line, engaged in nematode analysis of thousands of Dutch soil samples, and also the use of serology in surveying for virus diseases in plants. This last is particularly gratifying to me because at the time I first proposed that serology be used for this purpose, in 1937, one of the virus authorities in the United States rather aggressively attacked the practicability of this method of surveying. There is an active programme of plant disease surveying in Belgium under Dr Vandervalle aided by a useful collection of score-cards which are provided for the surveyors. It was encouraging to learn from Dr Morstatt in Germany that the records of the German Plant Protection Service survived the War and that this surveying activity, which had its origin in Sorauer's thinking nearly 50 years ago, continues to be active.

In Ireland results of a rather unusual type of survey have recently been published by Prof. Muskett. It involves a 10-year study of the state of health or disease of seeds in commerce, and illustrates admirably the fact that surveying may be a research tool, yielding new and important scientific conclusions.

The Canadian Plant Disease Survey is another excellent model, distinguished by its use of phenology in relation to plant disease outbreaks.

In the United States, our survey activities have not been as thorough and systematic as might be wished. However, special surveys have been made from time to time, and since the War this is being systematically done with certain diseases such as tobacco downy mildew and potato late blight.

The research and surveying that I have mentioned have been chiefly sponsored by the several governments concerned. It is encouraging to find that industry and private agriculture are also becoming interested in this problem. On the part of industry, this is illustrated by such activities as those of Mr Ordish of Imperial Chemical Industries, whose book, *Untaken Harvest*, has been a valuable contribution to this subject, and the annual cereal stem rust surveys that have been conducted for many years in the United States and Canada under the sponsorship of the grain industry.

As an example of what we call in the States a 'grass roots reaction', there was recently held in Texas a Cotton Disease Conference in which major attention was given to the measurement of plant-disease losses. There was a great deal of interested discussion on the part of cotton growers and ginners on the need for reliable determination of disease losses, and the group took steps to organize a comprehensive study to accomplish this.

I will not go into the means that are used to disseminate information on plant-disease losses in the several countries beyond mentioning one new development. I refer to the World Reporting Service of FAO in Rome, under the leadership of Dr Lee Ling. This serves as a clearing-house for information on plant disease and insect losses on a world-wide scale, implemented by the new journal, *Plant Protection Bulletin*, that is devoted to this purpose.

This much is being done, but so much more remains to be done. Activities such as I have mentioned need to be conducted more intensively and on a much broader scale. Our first problem is self-education, creating an awareness among agricultural scientists of the need for better information on losses. Next is a fuller recognition of the value of loss information by our governments so that our efforts may be recognized and strengthened. Isolated efforts are better than nothing, but it is so much more effective to have them organized on a national scale. As the work in the several countries grows there will be increasing need for international co-operation. Already we have the machinery for this: for co-operation in research on appraisal and survey methods through the International Commission on Plant Disease Losses and for exchange of loss information through the World Reporting Service of FAO.

Our colleagues who are engaged in thorough studies of individual diseases or diseases of individual crops should be encouraged to include methods and results of loss appraisal in their studies as a necessary part of any comprehensive plant disease investigation. Here is a field in which a number of young pathologists and entomologists might be encouraged to specialize, devoting their scientific careers to the economic aspects of plant pathology and entomology.

Studies conducted for other purposes will often yield valuable information on losses if the data taken are of the right sort and sufficiently complete. For example, over the years workers in Arkansas accumulated a large volume of data on the yields of cotton of different varieties and under different fertilizer treatments. These workers were not concerned with loss measurement; however, their data were sufficiently complete that it was possible to analyse them and reach a number of important conclusions respecting the tempo of wilt disease and the losses caused by it.

I hope we can look forward to having, eventually, a handbook of methods of appraising plant-disease losses. This might well be the joint effort of many workers, each of whom is familiar with specified diseases and best able to contribute material on those diseases. The International Commission on Plant Disease Losses is considering taking leadership in preparation of such a handbook. The handbook should contain standardized directions for taking data on disease occurrence and translating this into loss, in such fashion that the directions could be used by personnel engaged in agricultural survey work who have little or no training in plant pathology or understanding of plant disease hazards. These men, economists, agronomists, crop scouts, crop insurance adjustors, railroad agricultural representatives, and others, could profit by attending short courses of instruction designed to offer them simple yet reliable guidance in assessing plant disease problems for what they actually are, economically.

Finally, having in hand reliable and defensible statistics on the losses from plant diseases, the full benefits of this endeavour could be reaped by making available those statistics to the many individuals needing them, to agricultural administrators who need to know the most strategic points toward which research and educational resources should be directed, and who must substantiate their claims for support with reliable loss estimates, to industries that need to know the markets for their disease-preventive products, to the planners of new agricultural enterprises who must be advised of potential hazards, to the legislator, and to the man in the street, the consumer who, most of all, stands to profit by the reduction of crop losses and on whose goodwill and understanding the future of agricultural science depends.

Large, E. C. (1955). *Ann. appl. Biol.* **42**, 344–354

METHODS OF PLANT-DISEASE MEASUREMENT AND FORECASTING IN GREAT BRITAIN

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(With 4 Text-figures)

In speaking of 'methods' of plant-disease measurement in this country, I propose, first, to give a very brief review of the ways in which our present activities in this field have developed—to put them in some historical perspective—and then to illustrate some of our actual methods of mensuration, as they are adapted for the types of survey in which they are employed.

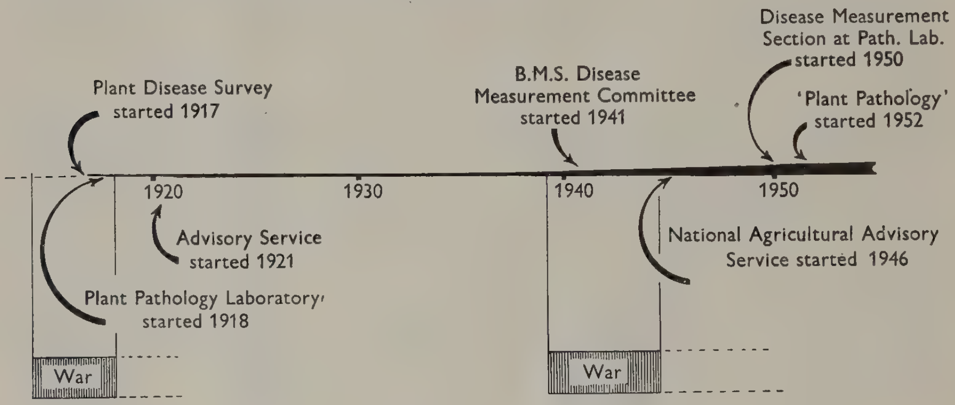
Plant Disease Survey started 1917
B.M.S. Disease Measurement Committee started 1941
Disease Measurement Section at Path. Lab. started 1950
'Plant Pathology' started 1952
1920
1930
1940
1950
Advisory Service started 1921
National Agricultural Advisory Service started 1946
Plant Pathology Laboratory started 1918
War
War

Fig. 1. Growth of plant disease survey work in England and Wales.

Fig. 1 shows some events of importance in the story. Our country-wide surveying of the occurrence of diseases in our crops started 37 years ago—in 1917, during the First World War. The records, provided mainly by the Advisory Service, have been collated by the Ministry's Plant Pathology Laboratory over the period and published in a sequence of bulletins. This surveying has provided very full information on the diseases present in the country, but until recent years it has rarely made it possible to arrive at any *quantitative* estimate of damage or loss. In 1941, during the Second World War, leading plant pathologists in this country, acting as a small committee of the British Mycological Society, set themselves to improve the system of surveying by devising simple but reasonably accurate practical methods of disease measurement. The first members of this committee were F. C. Bawden, R. W. Marsh, W. C. Moore and W. Buddin (secretary). With the help of many collaborators they drew up tentative keys and sampling procedures for a number of diseases (Moore, 1943). In 1949 this work on the evolution of methods was taken over by the present Disease Assessment Committee of the N.A.A.S. Conference of Plant Pathologists.

The next important steps, taken chiefly as a result of the drive and determination of W. C. Moore, were the starting up in 1950 of new sections of the Plant Pathology Laboratory, with officers appointed specifically for the promotion of both disease measurement and pest assessment, and, shortly after that, in 1952, the starting of a new scientific journal, *Plant Pathology*, edited at the Laboratory, having as one of its principal objects the publication of the results.

Thus we now have in this country a Disease Assessment Committee continuing the work of devising keys and survey methods; a Conference of Plant Pathologists in the N.A.A.S. undertaking projects in which the methods are applied in country-wide surveys which are a part of their general advisory work; and a section of the Plant Pathology Laboratory exclusively devoted to co-ordinating the work, collating the results, drawing in information from all available sources, linking it up with research, and publishing the whole, little by little—gradually building up the corpus of the subject, as a part of the Ministry's Intelligence Service.

Now, as to methods of assessment—the actual mensuration—I will, as it were, take you into our workshop and show you some of our jobs in hand. We have a number of projects, some well under way, a few even written up and already published in *Plant Pathology*, and some just beginning.

I will begin with one of our youngest: tulip fire. This may not be a disease of major economic importance, but it affects a valuable crop, and it will serve to illustrate the start of drawing up a disease measurement key. As, in some respects, there are no two plant diseases more similar than tulip fire and potato blight, it might be thought that our potato blight methods could be applied directly to tulip fire. But as soon as we look into the problem we find there is much more in it than *that*. Tulip fire has four phases: the sclerotial stage on the bulbs; the primary infectors (whose removal is the principal measure of control); the non-aggressive spotting (which can ruin a flower crop without material damage to the foliage); and lastly the aggressive attack on the foliage causing premature cessation of growth and reduction in the crop of bulbs. Any comprehensive scheme for the assessment of tulip fire must deal with each of these four phases. This brings me to my first point of general principle. Our whole experience since this work began in 1941 has led us to realize more and more clearly that attempts to devise portmanteaux methods for whole groups of diseases are a waste of time. Each disease must be studied individually, in the field, and throughout its course; the method of measurement for it must be based on acute observation of its idiosyncrasies.

Here is the beginning of the process for *one* of the phases of tulip fire: the aggressive phase on the foliage. We begin by collecting a number of plants in the field, at successive dates and showing varying degrees of infection. We dissect them, make working sketches of their parts to scale, and measure the leaf area and the area covered by lesions with a planimeter. In this process we discover many peculiarities of the disease. In tulip fire, for example, spores germinate in rain water trapped between the stem and the sessile leaf, causing a lesion girdling the stem at that point, and ultimately killing all parts of the plant above it.

The next stage in the evolution of an assessment key is to draw up a set of word pictures, or a diagram, by which varying degrees of percentage infection may be recognized easily in the field without dissection or measurement of the plant. Here, in tulip fire, a key diagram is being employed. And here may I make my second fundamental point:

For all foliage diseases our categories for degree of infection or decay refer, wherever possible, to the *percentage of the total green area of the plant rendered inoperative for photosynthesis by reason of the disease at the time of the observation*. That is a very important definition and statement of our aims. Since 1941 we have tried many systems of recording, using arbitrary grades, and subjective grades based more or less on the psychology of perception, but always, and however difficult it may be, we try in the end to assess the percentage of the foliage rendered inoperative for photosynthesis. That is meaningful information that later, with sufficient knowledge of crop growth, we may be able to use for the estimation of loss of produce. And it is *objective* information: other workers approaching the problem of measurement *ab initio* will obtain results directly comparable with ours.

Now, I would like to show you some sketches illustrating the growth of cereals. We are, of course, working on the estimation of rust and mildew in these crops, and we have found that it is necessary to have some precise way of defining the stages of growth at which the assessments are made. For this purpose, over the past 4 years, we have been using the Feekes scale for wheat (Feekes, 1941), with some modifications made by the late Dr Earnshaw at the N.I.A.B. to render it applicable also for barley, oats and rye, and with scale illustrations of the stages that I have drawn from plants in the field (Large, 1954). Incidentally, this chart has proved most useful, not only in disease measurement, but also in pest assessment, in varietal studies, and in defining the stages at which it is safe to apply growth-regulator weedkillers.

In the estimation of rust and mildew, as of other foliage diseases, there is one practical difficulty that must be overcome. How are we to distinguish between the effect of the disease and of normal senescence of the leaves? What is the use of estimating mildew on leaves that have already served their turn and are no longer operative for photosynthesis?

By defoliation experiments, and also by recording the state of each leaf (numbered downwards from the top) on a sufficient number of healthy plants of each cereal week by week throughout the growing period, we hope to be able to formulate a working rule for the number of leaves that are really operative for photosynthesis at each stage of growth. If we can do this it will greatly simplify the problem of mildew and rust assessment, and help us to proceed to the next step—of relating disease assessments to loss in yield. In this work such *physiological* studies as those of Watson & Norman (1939) and Porter, Pal & Martin (1950) must clearly be taken into account.

We are not satisfied with our field key for mildew in cereals, and we are working on its improvement. That is a normal part of our method. All our keys are provisional at first; they are subjected to years of practical test in the field, and they are amended in the light of experience.

Let me turn now, for courage, to a job that we have *done*. Perhaps the first fungus disease in this country, for which a true estimate of national loss has been obtained—and that by disease-measurement methods—is choke in cocksfoot seed crops (Large, 1954). In 1951, with the N.A.A.S. Grassland Officers and the Welsh Plant Breeding Station, we began a survey of *all* the cocksfoot seed crops of Aberystwyth strains entered for inspection each year. We used two methods. First an *extensive* survey method in which the inspectors rated the incidence of choked tillers in each crop as 'Absent', 'Occasional', 'Frequent', or 'Severe'; and secondly, an *intensive* method in which the plant pathologists sampled a random selection of about 10% of the crops, and *counted* the number of choked and healthy tillers in each sample. We found that the factor predominantly influencing the number of choked tillers was the age of the stand. There was very close agreement between the results of the two surveys, and the percentages obtained by counting in a random selection of the crops could be used to calibrate the subjective assessments of the inspectors. The mean loss of seed was found to range from less than 1½% in second-year crops, to 21% in the few old crops that had been down for 5–7 years. The overall loss for the whole country was about 3%. It is noteworthy that this quantitative survey, merely by showing where the greatest losses were occurring, at once brought about some reduction in the national loss caused by the disease. Old crops—many of which we found to be full of weeds and unproductive quite apart from their high level of choke—began to disappear.

Sometimes we have to deal with diseases that affect the *quality* of produce rather than the yield per acre. Then our work becomes 'blemish-assessment'. This is the case with common scab of potatoes. We began work on this disease in 1951, and after the usual step of examining, photographing and measuring a large number of affected tubers, we adopted a very simple key diagram for the assessment of this disease. Here the method is to imagine the tuber surface divided into eight parts, by lines drawn round it in each of three planes at right angles, and then to judge by eye how many eighths of the surface would be completely covered by the lesions if they were all crowded together. We found that what most observers regarded as a substantially affected tuber—to which the housewife would also take exception—was one having a quarter or more of its surface area affected (our '¼ scab'). This was in line with a definition already in use for surface diseases of tubers in our inspection work. When we came to employ our diagram in a national survey of common scab in collaboration with the Potato Division of the Ministry of Food, in

1952, we defined a substantially affected crop as one having 3% of the tubers with ¼ scab or over, *or* 50% of the tubers with ⅛ scab or over. Sample liftings were made on 2556 crops in 1952 and 2670 in 1953. The tubers were graded for scab according to our key diagram and weighed. Here advantage was taken of an existing crop sampling scheme—operating for the estimation of supplies—to obtain supplementary information on the incidence of disease. That is one of our 'methods'—always to seek our observations from those who have to visit, inspect, or sample crops for other purposes. It is not my purpose now to discuss the *results* of our surveys, but I will say that this work indicated that about 4% of the potatoes in this country had ¼ or more of their surface scabbed in the relatively dry season, 1952, and only about 2% in the wet season, 1953 (Large & Honey, 1955). It has shown the districts in which most of the scab occurs (Fig. 2) and provided data on relative susceptibility of varieties. The information is being used by Dr A. R. Wilson and his team of research workers at Sutton Bonington and it will also form the solid basis for field experiments on control in the future.

Another example involving blemish assessment is that of apple scab. Our aim from the first has been to devise simple field keys and to compare the assessments made by them, with those obtained by the more elaborate and time-consuming methods needed in research. Croxall, Gwynne & Jenkins (1952) have provided an admirable example of this in their work on apple scab. When assessing scab on fruit on the tree they take five branches per tree as sampling units. They find, for example, that small scab spots on about a quarter of the fruit on each unit equals 0·5% scab. This kind of assessment can be made very rapidly. They have compared it with a research method in which each individual fruit is graded by standard diagram and the mean infection calculated. They have found that the results by the two methods are in close agreement, and hence it becomes practicable to assess scab on a large number of trees, or in a number of orchards, with reasonable accuracy and no excessive expense of time.

A model piece of disease assessment work that has now been going on for 12 years in this country is that of Dr R. Hull, of Rothamsted (Hull, 1953), on the estimation of losses due to virus yellows in sugar beet. Here the method is based on the observed fact that 4–5% of the potential sugar yield is lost for every week during which the plants show yellows symptoms before mid-October. Checks are employed that I cannot now go into; I wish only to mention this important method, and to say that reliable estimates of loss are being obtained annually for the whole of the sugar-beet cultivation in this country. That is no small achievement.

Finally, I will give the briefest possible review of our work on potato blight. The basic work on the field key for this disease was done in 1941–3, and it has since been tested and retested so often that we can fairly say it is established. Using this key, and making simple eye assessments of the state of the haulm in observation fields at successive dates, we obtain our now familiar blight-progress curves (Large, 1952).

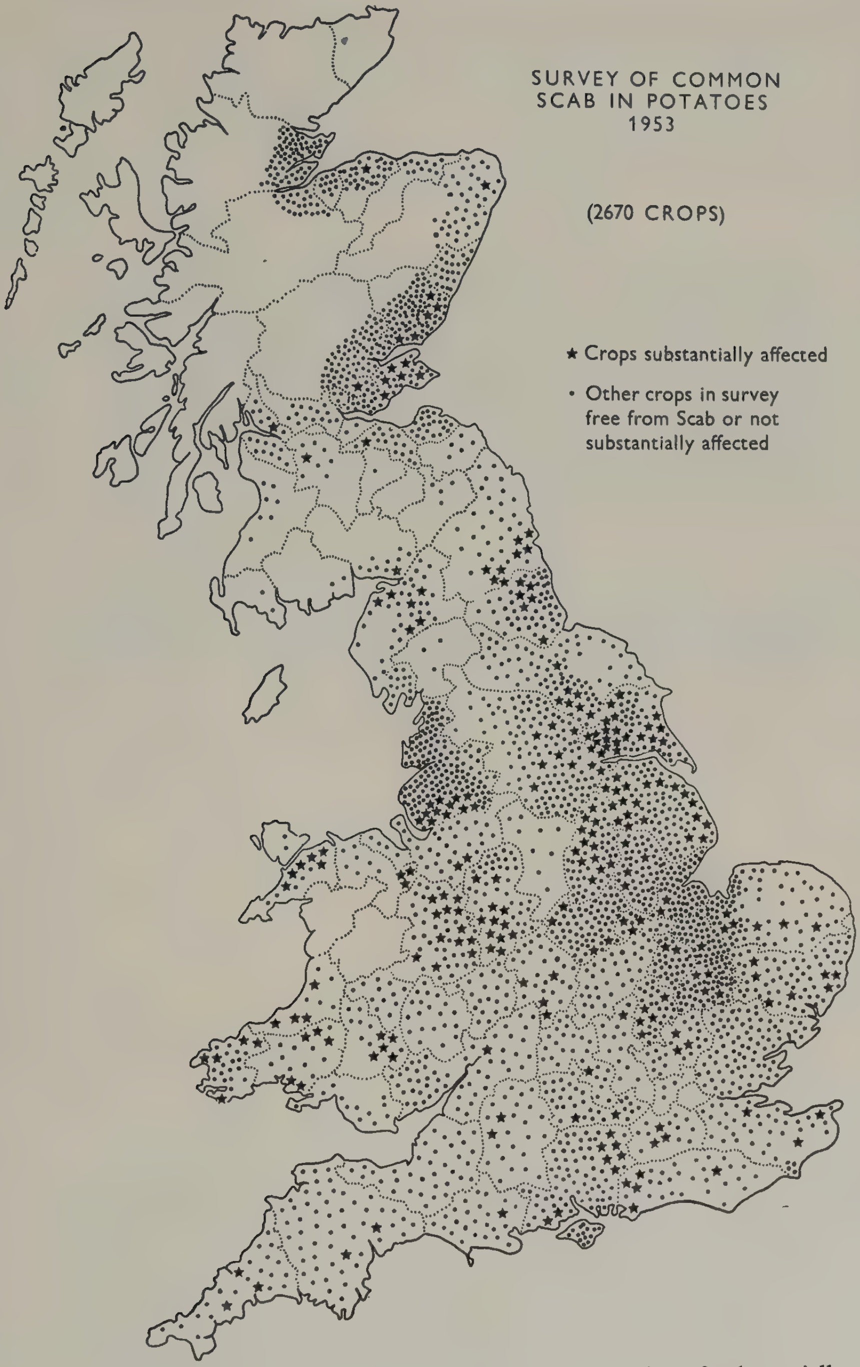
SURVEY OF COMMON
SCAB IN POTATOES
1953
(2670 CROPS)
★ Crops substantially affected
• Other crops in survey free from Scab or not substantially affected

Fig. 2. Extent of common scab survey in 1953, and location of substantially affected crops.

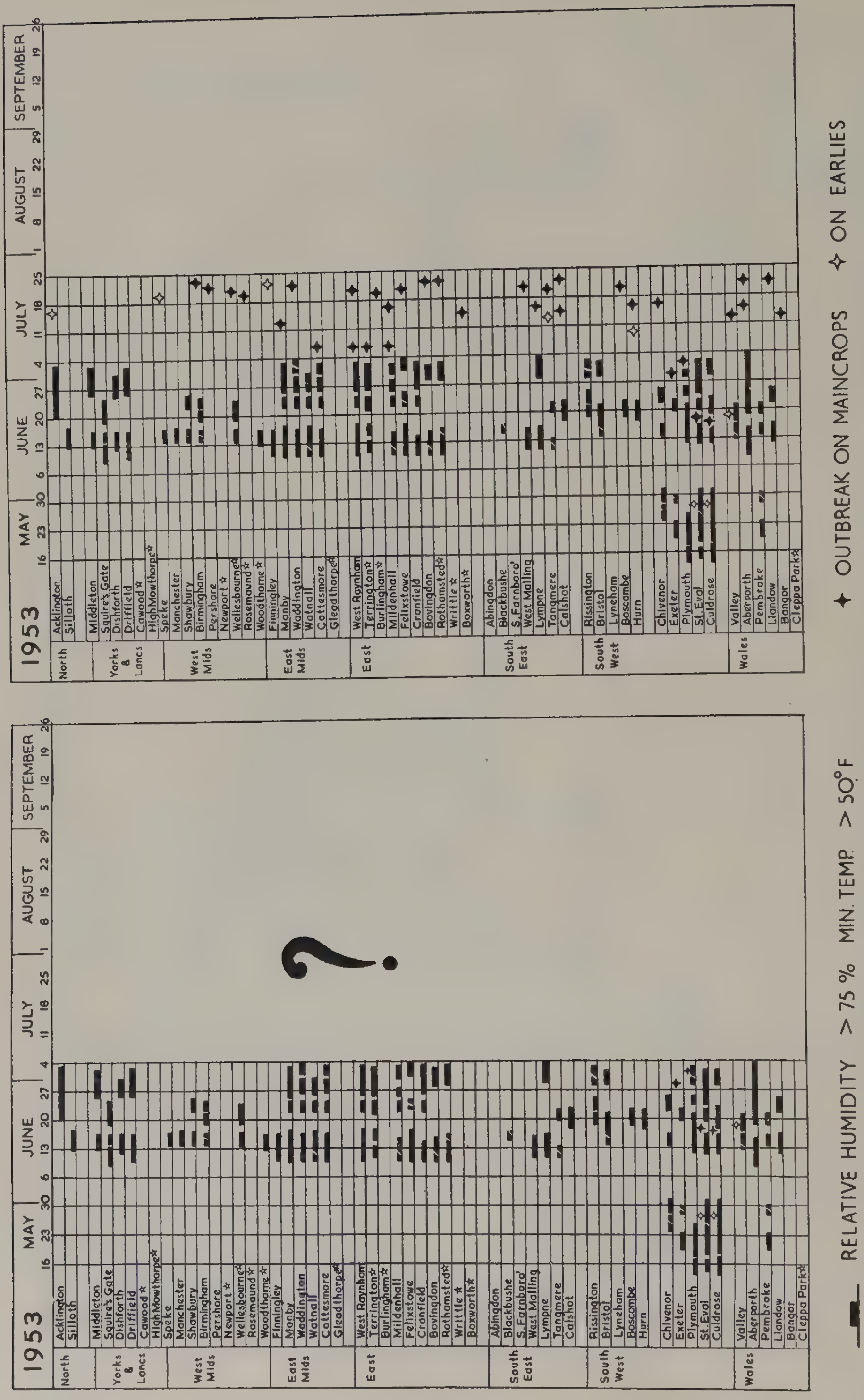

Fig. 3. The 'operations chart' method of potato blight forecasting. *Left*, chart at 4 July 1953, showing flush of warnings at end of June from which July outbreaks were forecast. *Right*, the chart 3 weeks later, showing the actual outbreaks reported.

Since 1950, we have been investigating the 'outbreak' or 0·1 % stage of the blight epidemics in great detail, for we have been testing the validity of forecasting by the Beaumont rule over the whole of England and Wales (Large, 1953). In this work, which is done in the closest collaboration with the Agricultural Branch of the Meteorological Office, the provincial plant pathologists are advised of the occurrence of Beaumont periods at some sixty weather stations, and they conduct searches in all areas for the first outbreaks of blight. Reports of outbreaks and the warnings are sent to the Plant Pathology Laboratory, where they are mapped and charted in relation to each other. During the season we are in constant communication by telephone with Mr L. P. Smith on the meteorological side, and at the end of each season we thresh out the performance of each station with him, in relation to its topographic situation, altitude, and other factors.

As our experience in the interpretation of the warnings increases, so the scheme is becoming more and more operational. Briefly, our method is not to rely on the indications of any one station, even for crops in its immediate locality; but to base our regional forecasts on the evidence provided by the whole network of stations as shown on an operations chart.

In 1953, for example, there was a flush of warnings about 13 June, but experience in previous years had taught us that such warnings were before 'zero date' for all regions except the south-west. It was on the second flush of warnings coming in the last week of June that we took action. We then sent copies of the chart to all the plant pathologists to advise them of the general situation, and issued a Press Notice, forecasting outbreaks in the east of the country early in July. This forecast was correct for the season (see Fig. 3).

In general, our forecasting by Beaumont rule is very successful for the main potato-growing districts, and for the July outbreaks which are of most importance for the timing of spraying. It is sometimes less successful for the central parts of the country where relatively few potatoes are grown, and for the later outbreaks. This arises from the fact that there are greater divergencies between the humidity conditions in the screens at the weather stations and those in the crops later in the year, and a number of our stations in the central area are on high ground. Relations between humidity conditions in the screens and in the crops are being investigated by Mr J. M. Hirst at Rothamsted; supplementary stations are used, and ways of overcoming the deficiencies of the system are being devised.

It is only in about one year in three that we have so early an epidemic in the east as that in 1953, and it is, of course, what happens *after* the outbreak—how fast or how slowly the attack progresses—that determines the loss caused by blight. In addition to our outbreak records, we obtain complete progress curves for representative crops in all parts of the country. From these curves we can now begin to assess the probable mean loss caused by blight each year in each district.

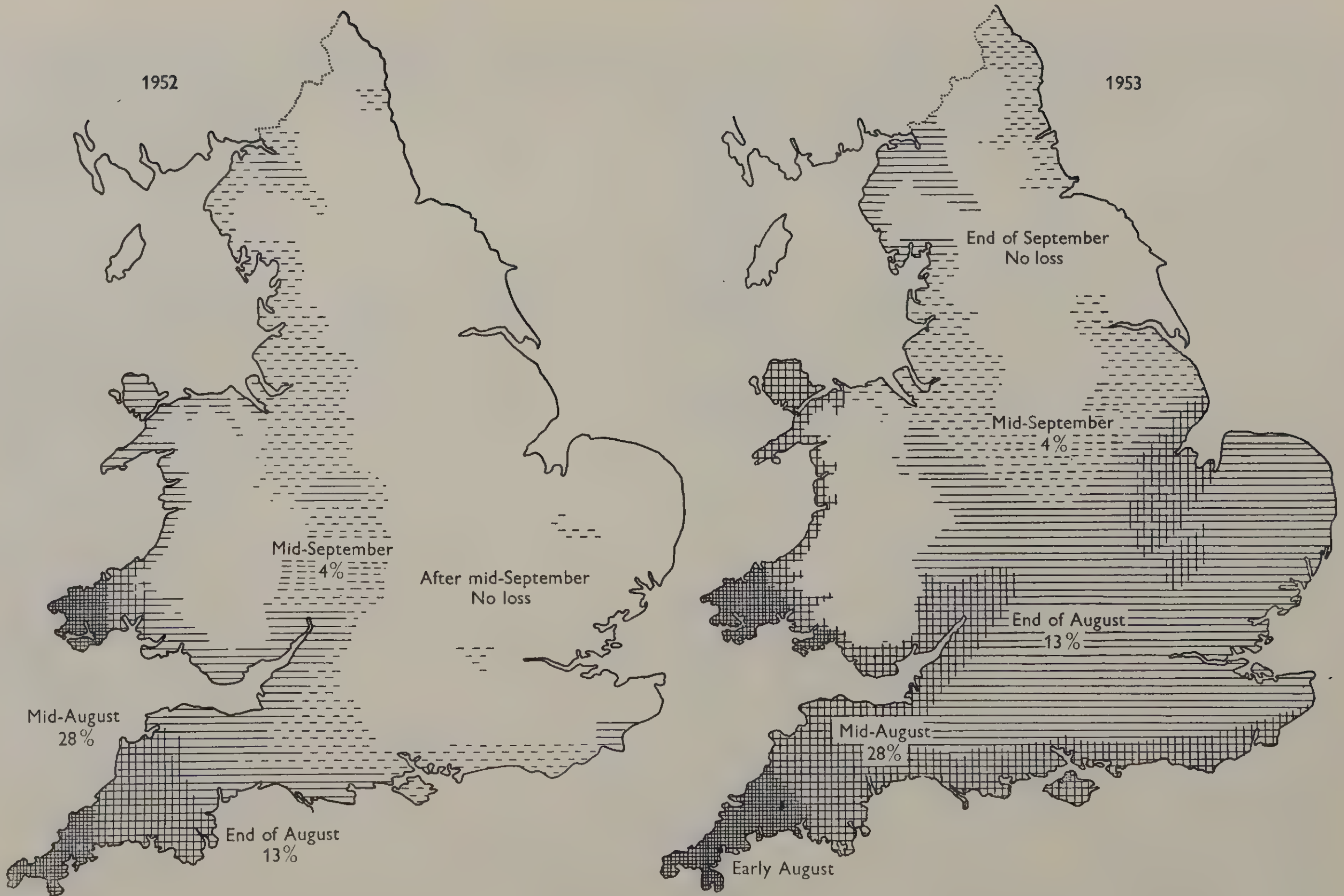
1952
Mid-September
4%
After mid-September
No loss
Mid-August
28%
End of August
13%
1953
End of September
No loss
Mid-September
4%
End of August
13%
Mid-August
28%
Early August

Fig. 4. Zoning of England and Wales according to dates at which the haulm of unsprayed maincrop potatoes reached the 75–90% blight stage in 1952 and 1953, with corresponding estimated mean losses due to premature stoppage of growth. Further losses due to blight infection of tubers are not included in the estimates.

There comes a time in the progress of the decay of the haulm when tuber production is stopped. Provisionally we take this as the 75 % stage. By projecting upwards from the 75 % date on to a mean curve derived from periodic liftings on a large number of crops we can read off the probable loss of potential crop due to the premature cessation of growth (Large, 1952). The validity of this method is being checked against the results of actual spraying trials at a number of centres over a long period of years. So far it has given results of the same degree of accuracy as lifting and weighing in randomized block layouts (Beaumont, Bant & Storey, 1953; Large, Taylor, Storey & Yule, 1954).

Our survey work now permits us to zone the country according to the dates at which the 75 % (or 75–90 %) stage is reached each year. Hence from our loss curve we can indicate the probable mean loss in each district due to premature death of the haulm—there are further losses due to blight in the tubers, but those are not here considered. Fig. 4 shows our tentative estimates for a typical 'blight year', 1953, and for a typical 'no-blight year' in the east, 1952. On average about one year in three is a 'blight year'.

Protective spraying could not by any means save the whole of the losses indicated on these maps. Wheel damage in spraying reduces the yield by at least 4 % (Large *et al.* 1954) and the spraying usually only retards the reaching of the 75 % stage by about a fortnight. We have also to bear in mind that in blight years our potato yields are generally above average despite the blight. Routine spraying tends to increase supplies in the bumper years when there is plenty of rain, and to diminish them in the years when supplies are short owing to dry weather.

Hence the great importance of our work on forecasting; its function is not only to help in the proper timing of spraying in the blight years, but to minimize the spraying in the other years when it causes positive loss.

REFERENCES

Beaumont, A., Bant, J. H. & Storey, I. F. (1953). Potato spraying trials in Yorkshire, 1947–51. *Plant Pathology*, **2**, 56–60.

Croxall, H. E., Gwynne, D. C. & Jenkins, J. E. E. (1952). The rapid assessment of apple scab on fruit. *Plant Pathology*, **1**, 89–92.

Feekes, W. (1941). De Tarwe en haar milieu. *Vers. XVII Tech. Tarwe Comm. Groningen*, pp. 560–1.

Hull, R. (1953). Assessment of losses in sugar beet due to virus yellows in Great Britain, 1942–52. *Plant Pathology*, **2**, 39–43.

Large, E. C. (1952). The interpretation of progress curves for potato blight and other plant diseases. *Plant Pathology*, **1**, 109–117.

Large, E. C. (1953). Potato blight forecasting investigation in England and Wales, 1950–52. *Plant Pathology*, **2**, 1–15.

Large, E. C. (1954). Surveys for choke (*Epichloe typhina*) in cocksfoot seed crops, 1951–3. *Plant Pathology*, **3**, 6–11.

Large, E. C. (1954). Growth stages in cereals. Illustration of the Feekes scale. *Plant Pathology*, **3** 128–9.

LARGE, E. C. & HONEY, JUNE K. (1955). Survey of common scab of potatoes in Great Britain, 1952 and 1953. *Plant Pathology*, **4**, 1–8.

LARGE, E. C., TAYLOR, R. ERIC, STOREY, I. F. & YULE, A. H. (1954). Spraying trials in the potato-growing area around the Wash, 1948–53. *Plant Pathology*, **3**, 40–8.

MOORE, W. C. (1943). The measurement of plant diseases in the field. *Trans. Brit. mycol. Soc.* **26**, 28–35.

PORTER, H. K., PAL, N. & MARTIN, R. V. (1950). Physiological studies in plant nutrition. XV. Assimilation of carbon by the ear of barley and its relation to the accumulation of dry matter in the grain. *Ann. Bot., Lond.*, N.S., **14**, 55–68.

WATSON, D. J. & NORMAN, A. G. (1939). Photosynthesis in the ear of barley and movement of nitrogen into the ear. *J. agric. Sci.* **29**, 321.

Hille Ris Lambers, D. (1955). *Ann. appl. Biol.* **42**, 355–360

POTATO APHIDS AND VIRUS DISEASES IN THE NETHERLANDS

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Although it was first discovered in the Netherlands that aphids transmit leaf-roll (Oortwijn Botjes, 1920) virus research was mainly concentrated on the virus, less on the vector. Elze (1927) wrote a paper on transmission experiments carried out under laboratory conditions, but extensive field work was not started until 1936. Then aphid counts were started by threshing plants over a board of 40 × 50 cm. Small numbers of aphids were counted directly on the board, large numbers were estimated by counting all aphids in some of the twenty squares in which the surface of the board was divided. Weekly counts showed clearly how the aphid population developed. By 1938 a number of field inspectors had been trained in aphid recognition and they sent in weekly reports from numerous localities over the country. These were mapped centrally and in this way a clear picture of the aphid situation all over the country was available.

It soon appeared that a year with many aphids (and much virus spread) was followed by a year with few aphids. This biennial rhythm had already been noted by Blattny (1925), in a completely overlooked paper. He explained it as follows: in a year with many aphids the enemies of aphids have an opportunity to multiply strongly, so that in the next year a comparatively large number of enemies is capable of keeping the aphid population at a low level. But then the situation is less favourable for the progeny of the aphid enemies, so that the following year the aphids are in a better position. In the Netherlands in the last 18 years the uneven years (notably 1939, 1947, 1951) were the years with many aphids.

An analysis of the aphid/aphid-enemies complex in potato fields was our first project. For this purpose the potato aphids, and those of their enemies which we found in potato fields were reared at various temperatures. The feeding capacity of the enemies from first-instar larvae on was studied. And finally the parasites and hyperparasites of the aphids and their insect predators were studied in the same way. Because the complex appeared to consist of well over fifty different insects of which some, e.g. Chrysopid larvae, also attacked their collaborators (Coccinellid larvae and young Syrphid larvae) we had to stop this type of work.

But we could obtain a general picture. When aphids arrived on the potatoes few enemies were present. Then the aphids built up a population and the more aphids there were present, the more enemies appeared. At a certain moment the enemies destroyed more aphids than were born and then the aphids decreased in number.

On an average this happened about 15 July. If the aphids had a good start, they occurred in masses and the curve dropped very sharply. But if the aphids were from the beginning hampered by enemies the curve rose slowly and also descended slowly, with sometimes small increases even in August.

From this it was clear that enemies, above all predators like Coccinellids and Syrphid larvae, played a very important role in the regulation of the aphid population, and therefore were not to be neglected.

The hibernation of the most important aphid, *Myzus* (*Nectarosiphon*) *persicae* (Sulzer) was known from the literature. The species hibernates as eggs on peach (and nectarine) in America also on wild *Prunus* spp., and in mild climates as viviparae on various herbaceous plants, e.g. in Great Britain.

In the Netherlands hibernation on herbaceous plants was only found once in the last 25 years. Colonies were often found up to January, but then they died out. Hibernation indoors often occurred on plants on window-sills, the pride of every Dutch housewife. On the whole this will have no influence on the infestation of potato fields, because these plants are rarely neglected. Glasshouses are worse in this respect. Mangold-clamps may be a source of infection, but *Myzus persicae* is certainly a very rare aphid in Dutch clamps when they are opened for the first time.

In 1946 we discovered that *M. persicae* hibernated successfully as eggs on the American bird cherry, *Prunus serotina*. It took some years to find out whether this method of hibernation was of any importance, but in a few years it was clear that older sheltered trees of this species could be very strongly infested in the spring. This is a problem of paramount importance, because in reforestation with *Pseudotsuga* and *Larix leptolepis* many millions of *Prunus serotina* were also planted, in areas where the peach is almost non-existent. In the southern half of the country there are more peaches, but in the northern half peach trees are rare and their complete eradication there was advocated by Quanjer.

It seems difficult to ascertain which influence must be ascribed to each of the two means of hibernating, but it is possible to find out where the alatae colonizing potatoes come from. Alatae from peach and *Prunus serotina* differ in morphology from those belonging to later generations, or from those born from a hibernating viviparous line (Gillette & Taylor, 1908). But the latter are so similar to alatae of three other species of the subgenus *Nectarosiphon* Schout. (species not re-recognized until 1945), that it was 1949 before all possible errors were eliminated. Then it appeared that during the migration period from winter host to summer host over 97 % of the alatae arriving on potato in early summer came from peach or *Prunus serotina*. The remaining 3 % might have belonged to a 4th generation leaving the winter host. Consequently, hibernation of herbaceous plants by viviparae is of little importance to the potato crop in the Netherlands.

We now could concentrate on the primary hosts. The number of eggs deposited in the autumn could not be observed directly. Several other aphids (*Rhopalosiphum* *nymphaeae* (L.), *R. padi* (L.), *Myzus lythri* (Schrank), *Hyalopterus pruni* (Geoffr.), *Phorodon humuli* (Schrank) lay numerous eggs on peach and *Prunus serotina* and we could recognize only the eggs of *Hyalopterus pruni*. But we could easily recognize adult oviparae of *Myzus persicae* and by multiplying their number with a factor we could estimate the number of their eggs. This, however, was not satisfactory. The percentage of eggs hatching in the spring varied very considerably and of the hatched young larvae almost all the earlier hatched ones died, especially on *Prunus serotina*. There was no simple relation between the number of eggs deposited in the autumn and the number of fundatrices reaching adulthood. So we counted fundatrices annually on the same trees.

Frequently the colonies founded by fundatrices were destroyed by predators before a single alata could fly away. In other years the complete progeny of one fundatrix, a few thousands of alatae, escaped unhindered. That depended on the activity of the predators. By enclosing primary colonies in a wide tube, just before alatae would develop, and by counting the escaping alatae, the importance of predators in that year could be measured. Of course direct observations on the numbers of Syrphids and Coccinellids were also made.

It was now possible to find the size of the migration to potato, and also to predict the development on potatoes, because the presence of a great number of predators in spring means that these will later prevent the aphids on potatoes from becoming too numerous. Moreover, the moment of migration was known. Because the speed of development of the aphids over a period of 2 months is about the same from year to year, the moment of migration enables one to state when the aphid population will reach its maximum.

All this is directly related to seed-potato growing in the Netherlands. There are two definite periods in the spread of leaf-roll. The early spread, always resulting in current season symptoms, is presumably caused by alatae flying from winter hosts to potatoes. It follows from Johnson's work (1953, 1955), that in this case no long-distance transport of virus occurs, so that early spread of leaf-roll is usually of no importance in areas where only healthy seed is used. The degree of early spread of leaf-roll can to some extent be predicted by the number of escaping alatae from the winter host, i.e. by multiplying the number of primary colonies by the number of escaping alatae per colony. Direct counts of alatae on potato during the migration period provide further evidence.

The main spread in the Netherlands occurs in July, by alatae developed on potatoes and other herbaceous plants. In this case there is short-distance as well as long-distance transport of leaf-roll virus, the latter presumably only by aphids born on already diseased plants. It is this second wave of infection which for about 150 years has determined some aspects of seed-potato growing in the Netherlands. As early as 1810 Friesian seed growers commented on the advantage of lifting seed potatoes early to prevent infection of the tubers with leaf-roll, then called 'the curl' of the potatoes. This practice has been continued until to-day and numerous data are available to prove its importance. Relating this to aphids, it means that the potatoes must be lifted before the aphids become too dangerous. A delay of a few days often means heavy infection with leaf-roll. On the other hand, in many years only a small crop is harvested, partly consisting of unripe tubers. About the time of early lifting the curve of yield against time is almost a straight line. It has been estimated that on an average the increase in yield per day per hectare around the early lifting day amounts to 700–1000 kg.

The best four grades of seed potatoes are not certified unless they have been lifted before a fixed date, the dates varying according to the potato variety, the grade and the region where the seed is grown. The dates for early lifting are annually fixed by the Nederlandse Algemene Keuringsdienst (N.A.K.). The regional organizations are free to fix an earlier date for their region and they can apply to the N.A.K. for a later date, which is only rarely granted. The difficulty is how to fix a date for early lifting months before the crop has to be lifted.

For many years the only basis has been the experience of the previous year. Samples of certified seed were and still are planted to judge the correctness of the measures applied the year before. After a disappointing harvest there was a tendency to prescribe an earlier date, which was, incidentally, rather reasonable from the virus point of view, because more sources of virus were available.

After more had become known about the aphids, it was possible to fix dates for early lifting on slightly more logical grounds. For it was possible by the end of May to predict whether in July there would be many aphids or few, and whether they would start to build up early or later than normal. The aphid forecast was then taken into consideration when the N.A.K. had to fix the dates for early lifting.

During a visit to England in 1945 we learned about the British method of studying aphid flight with traps. We wanted to do this also in the Netherlands, but in the meanwhile we had discovered that there are three other, very similar species of *Myzus*, none of them infesting potato, which occasionally are very numerous. The alatae of these species are almost indistinguishable from the 'summer' alatae of true *M. persicae*. It took 4 years before it was possible to identify the various alate *Myzus* sp. We did not like the sticky traps which Mrs Watson and Broadbent used and developed a suction trap driven by batteries.

Broadbent's paper (1950) on the correlation between the annual catches of alate *M. persicae* and the spread of leaf-roll near the traps gave the stimulus for further work in this direction. We reasoned that, since there was a correlation between the annual catches and the spread of leaf-roll per annum, there probably also existed a correlation between daily catches and the spread of leaf-roll per day. For this purpose very efficient traps were wanted. We finally chose the yellow traps as described by Moericke (1951), but slightly modified for our purpose. In the first year we stationed six traps in each of twenty-two fields. By sampling tubers twice a week the virus spread was measured. The traps were emptied daily before 9 o'clock and the catches mailed promptly. The catches had to be examined immediately after arrival. The traps catch many aphids, besides many other yellow- or water-loving insects. Sometimes up to 7000 aphids per trap per day were caught, and up to 1700 winged *M. persicae*.

The results of the first year have already given very interesting information. Like others we had not found an important correlation between aphid counts on the plants and the spread of leaf-roll in the same fields. In 1951 numbers of alate *M. persicae* turned up in traps in the north of the country in a period when the local potato growers felt quite safe because they had very few aphids in their crop. About 100 km. to the south-west a very large aphid population infested the potatoes in an area where leaf-roll was abundant. Weather conditions (thermal air-currents and a south-western wind) made it probable that the alatae were transported over about 100 km. The subsequent explosion of leaf-roll in the northern area stood in no relation to the number of aphids present on the potatoes. Experiments with Systox against the spread of aphid-borne virus diseases further confirmed the supreme importance of flying aphids as vectors of virus. These alatae were, in summer, not correctly estimated by counting on the plants. All this made it clear that correlation need not exist between number of aphids on the plant and virus spread in the fields where the counts were made.

Counting on the plants was continued, but on a smaller scale. For it still gave us some idea of the number of flying aphids we might expect, even if these alatae would land elsewhere. But the trapping scheme had to be enlarged, so that more data from more localities would be available.

The greatest obstacles were the immense number of trapped aphids and the occurrence of the three *Myzus* species very strongly resembling *M. persicae*, species which could be rather numerous and which often started flying just before *M. persicae*.

The first trapping season taught us that the customary methods of aphid determination after clearing and mounting could not be used. But with a pocket-lens magnifying 6 times it appeared to be possible to recognize most aphid species easily, and in many cases easier than in the best mounts. Therefore groups of analysts from the laboratories of the Regional Inspection Services of the N.A.K., most of whom knew nothing about insects, were trained in the recognition of *M. persicae*, which took 2½ days per group. They do their work surprisingly well, but we still re-examine every single catch, mainly because of the related *Myzus* species. The total number of traps could be increased from year to year as more trained help became available. As the variation in catches between six traps in the same field was very small, we reduced the number to two traps per field which gave us data from more localities.

The practical results are the following. Dates for early lifting, partly based on a long-term aphid forecast are still prescribed. The trap catches enable us to warn regions where the flight of *M. persicae* (and other potato aphids) reaches a critical level. But also neighbouring regions must be warned of the danger, because the aphids may go their way. All aphid catches have to be dealt with on the date of arrival. At 5 p.m. a report is sent out to all Regional Inspection Services, containing the analyses of the catches in the whole country. These reports are strictly confidential, because the trade might be inclined to buy from areas where few potato aphids were trapped. After a warning the Services have some time left in which to take measures, because the virus has to pass from infection points to the tubers.

As we pointed out earlier, the advantage of postponing lifting to the last possible day can easily be expressed in money. And the sums involved in the whole scheme represent only a very small fraction of the potential profits. This is generally realized so that from the start till to-day the number of aphid traps had to be strictly limited to a maximum, at present 220 traps.

It is probable that the combination of long-term aphid forecasts, combined with the present warning system has given a more rational basis to the Dutch early-lifting policy, though much still remains to be done.

REFERENCES

ANON., (1810). *Magazijn van Nederlandschen landbouw* **5**, 357.

BLATTNY, C. (1925). *Tijdschr. PlZiekt.* **31**, 139–44.

BROADBENT, L. (1950). *Ann. appl. Biol.* **37**, 58–65.

ELZE, D. L. (1927). De verspreiding van virusziekten van de aardappel (*Solanum tuberosum* L.) door insecten. Thesis Agricultural University, Wageningen.

GILLETTE, C. P. & TAYLOR, E. P. (1908). *Bull. Colo. agric. Exp. Sta.* no. 133, 34.

JOHNSON, B. (1953). *Nature, Lond.*, **172**, 813.

JOHNSON, B. (1955). *Proceedings 2nd Conference on potato virus diseases, Wageningen-Lisse* 1954 (in the Press).

MOERICKE, V. (1951). *Nachrichtenbl. deutsch. Pflanzenschutzd.* 3rd year, no. 2.

OORTWIJN BOTJES, J. G. (1920). De bladrolziekte van de aardappelplant. Thesis Agricultural University, Wageningen.

Plant nematodes

PETERS, B. G. (1955). *Ann. appl. Biol.* **42**, 363–371

NEMATOLOGY IN RETROSPECT AND PROSPECT

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The first small nematodes to be described, free-living in the seventeenth century and plant-parasitic in the eighteenth, are identifiable only from their peculiar habitats; taxonomy came relatively late in nematology because adequate optical equipment was a prerequisite. In the study of the free-living and the plant-parasitic species, the development of two readily-presented aspects of taxonomy, figure drawing and mensuration (each showing oscillation between paucity and excess of detail), is traced in the work of five founders, all of whom were living in 1904: Bastian, Bütschli, de Man, Cobb and Goodey. Possible future developments in the identification of species and strains, the investigation of host-parasite relationships, and the training of nematologists are briefly discussed.

During this Conference some speakers are taking the Jubilee of our Association as an occasion for looking back over the past 50 years, sizing up the present position of their subject, and peering prophetically into the future. I hope I may be excused if I depart somewhat from this formula by probing the more remote past, from the origins of our subject down to the present century, and by restricting my forward-peering within very modest limits. My excuse must be that the recent past is kept before us by text-books and abstracting periodicals. Some of the work of the 11 years from 1940 was surveyed by Chitwood & Oteifa in 1952. According to them, by that date the bibliography on phytoparasitic nematodes alone had increased to 3400 titles. I do not wish to survey so vast a literature, since it would involve reading it, but a brief account of some of the early work may be not uninteresting.

The word 'nematology' itself almost certainly did not exist in 1904, the year of our foundation. Cobb was using it by 1914 when he published the first of his fifteen 'Contributions to a science of nematology', whereas in 1890 he had used 'nematelminthology'. And one of his last acts was to publish in 1932 a stout defence of: 'The English word "Nema"' (as his paper was boldly entitled). Here he listed a number of verbal compounds of nema, including 'nematology' and 'nematicide'—spelt with two i's. But if the word nematology is modern, some knowledge of nematodes goes back at least to Hippocrates, giving us ample scope for retrospection.

As a subdivision of zoology confined to a study of nematodes, nematology is a tidier discipline than helminthology, which also covers flatworms, acanthocephalans, and other odds and ends. Even thus restricted, however, nematology tends to fall into two parts, for the practical reason that one man is likely to be mainly concerned with the nematode parasites of vertebrates, while another man, often with a different training, studies the plant-parasitic and free-living species. The word nematology is such a useful substitute for the clumsy phrase: 'Study of plant-parasitic and free-living nematodes' that it is now tending to assume that restricted meaning in some quarters. For several reasons I shall use it mainly in this narrow sense to-day, but we should not forget that in fact it covers all nematodes.

Our present phylum Nematoda contains over 1000 genera and several thousand species, a mere handful of which were known before the nineteenth century. This comparative ignorance of the early naturalists is due, first, to the small size of most nematodes and, secondly, to the fact that even large nematodes of one size look much alike externally: far more than in most other phyla we rely for differentiation on internal morphology. For both reasons, nematology had to await the invention of the compound microscope. This occurred early in the seventeenth century, but for another 200 years the compound microscope was optically poor: the problem of dealing simultaneously with spherical and chromatic aberrations in lens systems was not solved until 1830, when the father of Lord Lister showed how to combine two achromatic lenses so as to balance their spherical aberration. Thus, while the microscopists of the seventeenth and eighteenth centuries made fascinating discoveries, the best of them, Leeuwenhoek, used simple lenses which he himself ground; having magnifications from 50 to 200 diameters, they probably yielded a clearer image than any compound microscope of the time.

Seventeenth century

One of the earliest accounts of a free-living nematode was given in 1656 by Petrus Borellus in his 'Century of microscopical observations' (where 'century' is used as in cricket, and not of time). His first observation concerns the vinegar eelworm, which became a favourite object of study to the microscopists. He noted that it comes to the surface of the liquid in order to breathe. Robert Hooke, in his *Micrographia* (1665), made two interesting comments on these worms: first, that 'The wrigling motion of their body seem'd to be only upwards and downwards, whereas that of eels is only side wayes'; and secondly, that their slow progress was explicable by their small size and the low viscosity of the medium 'For what a vastly greater proportion have they of their superficies to their bulk, then Eels or other larger fishes' (an early comment on the surface/volume ratio). Leeuwenhoek found them more resistant than his animalcules to a concoction of pepper-water; somehow he even dissected the larger worms, finding them to contain globules, which he rightly claimed to be oil, and also very small worms coiled up. He used this last observation to support biogenesis against the spontaneous-generation school. The seventeenth century, then, gives us interesting comments on one free-living species, but there is no taxonomy: we recognize the species from its habitat.

Eighteenth century

It is a similar story in the eighteenth century, when again we recognize our first plant-parasitic species from its peculiar habitat. The observation, which marks the beginning of plant nematology, is due to John Turberville Needham in a letter to the Royal Society in 1743. He writes:

> Upon opening lately the small black grains of smutty wheat, which is here distinguished from blighted corn, the latter affording nothing but a black dust, into which the whole substance of the ear is converted, he perceived a soft white fibrous substance, a small portion of which he placed on the object plate: it seemed to consist wholly of longitudinal fibres bundled together, and without any the least sign of life or motion. He dropped a globule of water on it, to try if the parts, when separated, might be viewed more conveniently; when, to his great surprise, these imaginary fibres, as it were, instantly separated from each other, took life, moved irregularly, not with a progressive, but twisting motion; and so continued for the space of 9 or 10 hours, when he threw them away. He is satisfied they are a species of aquatic animals, and may be denominated worms, eels, or serpents, which they much resemble. He repeated the experiment several times, with the same success, and gratified others with a sight of it.

This animal was not named for over 50 years, but in 1799 Steinbuch is said to have included it as *Vibrio tritici* along with his *V. agrostis*. And it was another 50 years before the life history was worked out, by Davaine in 1857.

This paucity of taxonomic information on nematodes is well illustrated by Linnaeus's *Systema naturae*. In the 10th edition of 1758 (the *fons et origo* of zoological nomenclature) are three recognizable nematodes, all parasites of man. In 1767 the 12th edition adds the vinegar and sour paste eelworms regarded as one species, *Chaos redivivum*. But an interleaved copy in the Linnaean Society's library, annotated by Linnaeus himself, adds in manuscript the ear cockle nematode as *Gordius triticeus*.

The eighteenth century added a very few more free-living nematodes. There was considered to be a species in fresh and another in salt water, given trivial names like *fluvialis* and *marinus*, and placed, with the vinegar and sour paste eelworms, in one genus *Vibrio* or later *Anguillula*. But again these are differentiated merely by habitat.

Nineteenth century

The general foundations of systematic helminthology were laid down in the first half of the nineteenth century, in a series of major works by Rudolphi, Dujardin, Diesing and others. Dujardin's great work of 1845, *Histoire naturelle des helminthes* gave us, amongst other things, what have since become two of the largest of nematode genera, *Dorylaimus* and *Rhabditis*. But, while *Rhabditis terricola* is described with some taxonomic rigour, Dujardin inexplicably puts into the same genus *Vibrio tritici* and the vinegar and sour paste eelworms.

Nematology in our restricted sense can be said to have arisen in the 50 years preceding the foundation of our Association in 1904. By that date fourteen species of plant-parasitic nematodes were known, in the three genera *Tylenchus*, *Heterodera* and *Aphelenchus*. It may be of interest to see them listed under their original names, and grouped under the three genera in date order (Table 1). In addition, several species of *Tylenchus*, and *Aphelenchus* were suspect as being associated with plant roots. Most of the commoner genera of free-living soil nematodes had been established: *Diplogaster* by Schultze in 1857, and *Cephalobus*, *Monhystera*, *Mononchus*, *Plectus* and *Tripyla* by Bastian in 1865.

TABLE 1. *Plant-parasitic nematodes in* 1904

A. Genus *Tylenchus*
  (1) *Vibrio agrostis* Steinbuch, 1799
  (2) *V. tritici* Steinbuch, 1799
  (3) *V. graminis* Hardy, 1850
  (4) *Anguillula dipsaci* Kühn, 1858
  (5) *A. radicicola* Greeff, 1872
  (6) *Tylenchus millefolii* Löw, 1874
  (7) *T. pratensis* de Man, 1881
  (8) *T. fucicola* de Man, 1892
  (9) *T. similis* Cobb, 1893

B. Genus *Heterodera*
  (1) *Heterodera schachtii* Schmidt, 1871
  (2) *Anguillula marioni* Cornu, 1879
  (3) *Heterodera göttingiana* Liebscher, 1892

C. Genus *Aphelenchus*
  (1) *Aphelenchus fragariae* Ritzema Bos, 1891
  (2) *A. olesistus* Ritzema Bos, 1893

Among the pioneer nematologists still living in 1904 were Bastian, Bütschli, Cobb, Kühn, von Linstow, de Man and Marcinowski. Living, but not yet publishing, were Ditlevsen, Goodey and Micoletzky. It is a formidable list, drawn from many countries; the contributions they made to our subject were too multifarious for adequate summary in the time available. However, I should like to select five of them for special tribute as founders of our subject and at the same time to call attention to the progress made in two related aspects of taxonomy, namely the drawings used in illustrating nematode morphology, and the method of presenting measurements. For this purpose it would be advantageous to show the same species of nematode handled by the different nematologists, and a convenient example is the predaceous soil form *Mononchus papillatus*, of which the male was unknown until 1924.

H. C. Bastian, 1837–1915

Henry Charlton Bastian, Professor of Anatomy at University College, London, published in 1865 his 'Monograph on the Anguillulidae or free nematoids, marine, land and freshwater, with descriptions of 100 new species'. Nematodes were Bastian's hobby and this first-class work is the finest of his very few nematological writings. Among the 100 new species is *Mononchus papillatus*. In the lavishly produced plates, each figure is sparely drawn showing the main organs in outline only, and with a minimum of detail,—sufficient to differentiate the species then known, but barely adequate for dealing with species added later.

His measurements of this species, in fractions of an inch, give the length as 1/11, breadth 1/250, pharynx 1/714, oesophagus 1/4 of the body length, anus 1/166 from the posterior end, vulva at the beginning of the posterior 1/3. The modern worker requires a table of reciprocals to interpret this system, which has little to recommend it.

J. A. O. Bütschli, 1848–1920

Johann Adam Otto Bütschli was Professor of Zoology in the University of Heidelberg. His helminthological papers, published over a long period of years, include his 1873 'Beiträge zur Kenntniss der freilebenden Nematoden', which contains a figure of *M. papillatus*. It is at once evident that Bütschli either was himself, or used the services of, a better draughtsman than Bastian. There is far more detail in, for example, the mouth region, the pharynx, and the anal region. Moreover, Bütschli more often than Bastian took up space to draw the entire worm instead of merely head and tail regions.

Bütschli's text does not give detailed measurements of this particular species, but in general he gives length and greatest breadth in millimetres, and then oesophagus and tail length as fractions of the total length, thus emphasizing relative proportions rather than absolute dimensions, e.g. 1/4, 1/15. The level of the vulva is measured from the posterior end and then expressed as a fraction of the total length, e.g. 2/5. This is a great advance on Bastian's system. The fractions may be thought troublesome: they were simplified in two different ways by the two authors who now follow.

J. G. de Man, 1850–1930

Johannes Govertus de Man, curator at the Leyden Museum, spread his interests between the decapod crustacea and nematodes. Of his numerous and important contributions to nematology, best known is his monograph of 1884. This is in German but he wrote with equal facility in Dutch, French and English. The plates, with a somewhat abbreviated text, were re-issued in 1919. His drawings are clear but rather less detailed than Bütschli's, i.e. he omitted detail which he considered inessential.

De Man made extensive use of dichotomous keys. In his measurements he dealt with Bütschli's fractions by inverting them. Thus, for *M. papillatus* he gives the length as 2·6 mm., then follow: α (length divided by greatest breadth) 25–35, where Bütschli might have written 1/25 to 1/35; β (length by oesophageal length) $4\text{–}4\frac{1}{2}$; and γ (length by tail length) 15–25. The vulva is described as near the beginning of the posterior 1/3, which is in effect the Bütschli system uninverted. De Man's system is, of course, in wide current use with a, b, c, replacing α, β, γ, and the level of the vulva being measured from the anterior end and expressed as a percentage of the total length. Thus, in the ratios a, b and c the total length is numerator; in V it is denominator.

N. A. Cobb, 1859–1932

Nathan Augustus Cobb was born in Massachusetts and completed his helminthological training in Germany. After serving for many years in Australia as a general helminthologist, in 1904 he went to Hawaii for 3 years, after which he spent an active 25 years in the U.S. Bureau of Plant Industry, where he became chief and largely the creator of the Division of Nematology.

It is not difficult to laugh at Cobb. His great energy and enthusiasm carried him to over-emphasis and an exuberance of invention. But merely to laugh would be a mistake. Among our many debts to him are: (*a*) methods of quantitative soil sampling for nematodes; (*b*) separation of nematodes from soil by a combination of wet-sifting and sedimentation; (*c*) methods of killing by heat and processing without distortion in his 'differentiator'; (*d*) mounting nematodes between two cover-slips so that a second oil-immersion objective can be used as condenser; (*e*) technique for securing *en face* views of the nematode head.

In his 1917 monograph, 'The Mononchs', is included a highly detailed drawing of *M. papillatus*: a critic might say it was over-detailed. Accompanying it is the Cobb 'formula' which he began using in about 1890. In this formula are two rows of five numbers each. The upper row represents the distances from the anterior end to the following five levels: (*a*) posterior end of pharynx, (*b*) nerve ring, (*c*) posterior end of oesophagus, (*d*) vulva, (*e*) anus. The corresponding numbers in the second row are the body diameters at each level. All ten numbers are in percentages of the total length, which is given in millimetres at the end of the formula. Thus, for *M. papillatus* the formula is:

$$\frac{3 \qquad 9{\cdot}3 \qquad 26 \qquad 62 \qquad 93}{2{\cdot}6 \qquad 3{\cdot}5 \qquad 3{\cdot}8 \qquad 4{\cdot}3 \qquad 2{\cdot}4} \quad 1{\cdot}1\ \text{mm.}$$

With squared graph paper the proportions of the worm can be rapidly sketched in, or the absolute dimensions are readily got by multiplying throughout by one-hundredth of the length.

Unfortunately, Cobb could not leave well alone, and the formula was successively cluttered up with more and more symbols relating to striation, mouth and pharynx features, gonads, spicules, until it approached a complete description of the worm—and became a printer's headache. But, shorn of its excesses, it is simple, logical, concise and informative, and I for one would like to be told in what way the de Man system is preferable.

T. Goodey, 1885–1953

At this time I do not propose to pay any detailed tribute to the memory of Tom Goodey, a past President of our Association. This has been done elsewhere. Perhaps his death is too recent for us to see his work in its true perspective. However, I feel that it would be tantamount to distortion to omit his name from this short list of the founders of nematology. In matters of mensuration, he followed the de Man system. In figure drawing he deliberately aimed at less detail than Cobb, feeling that the morphological essentials should not be in danger of becoming obscured by a mass of detail. While his *Soil and freshwater nematodes* contains excellent figures for the head and tails of *M. papillatus*, their purpose is merely to illustrate a typical *Mononchus* and it would be not quite fair to compare them with the 'full-dress' drawings of the previous authors. Instead, Goodey's art can be well exemplified by one of his drawings for the *Phil. Trans.* paper on *Tylenchinema oscinellae* in *Oscinella frit*.

I have tried to show how, from late beginnings (late because of optical crudity), nematology on its plant and free-living sides has grown to its present stature in barely 100 years, largely through the efforts of men like Bastian, Bütschli, de Man, Cobb and Goodey. Figure drawing and systems of measurement, selected as easily presented aspects of taxonomy, are typical of scientific progress in that they both show a regular oscillation between insufficiency of useful detail and excess. If my emphasis has been taxonomic this is because taxonomy is the essential basis of our subject, and because later speakers will be dealing with experimental aspects.

The future

Looking briefly into the future, by way of conclusion, I would suggest that we have not yet exhausted all the available resources of the modern light microscope. If phase-contrast and polarization have given disappointing results hitherto, there may yet be limited fields for their useful application. The differentiation of species has come to depend on finer and finer morphological minutiae, and that process will undoubtedly continue. There remain cases, like the biological strains of *Ditylenchus dipsaci* and of some species of *Heterodera*, where morphological differentiation may always fail us. But if these strains do not differ in visible morphology they must at least differ biochemically, possibly in their constituent proteins. This suggests that a new field ready for development may lie in applying serological techniques to strain differentiation. In the complex inter-relationships between parasite and host, again, an approach from plant and nematode physiology and biochemistry is desirable. If this asks too much of the nematologist, then the remedy must lie in team work (difficult though this may be to reconcile with the requirements of Ph.D. students).

Lastly, this leads to the vexed question of the training of nematologists, with its vicious circle: there are few posts for nematologists because there are no trained nematologists to fill them; nematologists are not trained because there are few available posts. Probably training should be mainly post-graduate, but it is essential that the undergraduate should realize that there are nematodes other than *Ascaris lumbricoides*. The post-graduate training available at research stations is mainly applied and experimental in character, and there is urgent need for a department of nematology at one at least of the British universities, comparable with the Department of Plant Nematology in the University of California, in which full attention could be given to taxonomy, under a teacher who had time to specialize in the subject. At present, departments like the one at Rothamsted have to cover taxonomy as well as the applied and experimental aspects.

As is natural, the parasites of man and of his domesticated animals were the first nematodes to receive attention. The department to which I belong traces its origin back to the helminthology department in the old London School of Tropical Medicine, where Prof. Leiper insisted that nematodes of all kinds should be proper objects of study. This medical link is again obvious in our best bibliographical source: the *Index-Catalogue of medical and veterinary zoology* of the U.S. Department of Agriculture, a monument to the patient labours of Stiles and Hassall. But many nematologists have arrived by way of pure zoology or botany, entomology, or plant pathology. And this variety of approach is an advantage in a subject with so many aspects and with so many problems awaiting solution.

I am indebted to the Librarians of the Royal Society and the Linaean Society for their courteous assistance, and to the Librarian of Rothamsted who coped with the Dog-Latin of Borellus.

REFERENCES

BASTIAN, H. C. (1865). Monograph on the Anguillulidae or free nematoids, marine, land and freshwater, with descriptions of 100 new species. *Trans. Linn. Soc. Lond.* **25**, 73.

BORELLUS, P. (1656). *Observationum microcospicarum centuria.* Hagae-Comitum.

BÜTSCHLI, O. (1873). Beiträge zur Kenntniss der freilebenden Nematoden. *Nova Acta Leop. Carol. dtsch. Akad. Naturf.* **36**, 1.

CHITWOOD, B. G. & OTEIFA, B. A. (1952). Nematodes parasitic on plants. *Ann. Rev. Microbiol.* **6**, 151.

COBB, N. A. (1890). Arabian nematodes. *Proc. Linn. Soc. N.S.W.* 2S, **5**, 449.

COBB, N. A. (1914). *Antarctic marine free-living nematodes of the Shackleton expedition* (*Contributions to a science of nematology*, I). Baltimore.

COBB, N. A. (1917). The Mononchs (*Mononchus* Bastian 1866). A genus of free-living predatory nematodes. *Soil Sci.* **3**, 431.

COBB, N. A. (1918). Estimating the nema population of the soil. *Agric. Tech. Circ. U.S.D.A. Bur. Pl. Ind.* no. 1. 48 pp.

COBB, N. A. (1932). The English word 'Nema'. *J. Amer. med. Ass.* **98**, 75.

DAVAINE, C. J. (1857). Recherches sur l'anguillule du blé niellé considérée au point de vue de l'histoire naturelle et de l'agriculture. *C.R. Soc. Biol., Paris*, 2S, **3**, (Mém.), 201.

DOBELL, C. (1932). *Antony van Leeuwenhoek and his 'little animals'.* London.

DUJARDIN, F. (1845). *Histoire naturelle des helminthes ou vers intestinaux.* Paris.

GOODEY, T. (1930). On a remarkable new nematode *Tylenchinema oscinellae* gen. et sp.n., parasitic in the frit-fly, *Oscinella frit* L., attacking oats. *Phil. Trans.* B, **218**, 315.

GOODEY, T. (1951). *Soil and freshwater nematodes.* London.

HOOKE, R. (1665). *Micrographia: or some physiological descriptions of minute bodies made by magnifying glasses. With observations and inquiries thereupon.* London.

LINNAEUS, C. (1758, 1767). *Systema naturae*, 10th & 12th editions. Holmiae.

MAN, J. G. DE (1884). *Die frei in der reinen Erde und im süssen Wasser lebenden Nematoden der niederländischen Fauna.* Leyden.

NEEDHAM, T. (1743). Concerning certain chalky tubulous concretions, called malm; with some microscopical observations on the farina of the red lilly, and of worms discovered in smutty corn. *Phil. Trans.* **42**, 634.

STEINBUCH, J. G. (1799). Das grasälchen, *Vibrio agrostis*. *Naturforscher*, **28**, 233. (Not seen.)

JONES, F. G. W. (1955). *Ann. appl. Biol.* **42**, 372–381

QUANTITATIVE METHODS IN NEMATOLOGY

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(With 4 Text-figures)

The quantitative methods associated with nematology may be placed in four main groups:

(1) Estimation of soil populations.
(2) Assay techniques for the estimation of cyst contents.
(3) Estimation of eelworms on or within plants.
(4) Quantitative morphology.

The first three methods are now in general use and each will be considered in turn below. With the last, little progress has been made, although measurements have long been used in nematology to aid the separation of closely allied species. The most important work in this field is that of Fenwick & Franklin (1942, 1951) who, employing the simplest morphological attribute of nematodes, namely body length, devised a standardized technique for the measurement of larval length of *Heterodera* spp. and estimated the length parameters for eight species and varieties.

SOIL POPULATION ESTIMATION

The estimation of soil populations, which dates from Cobb (1918), now forms an important part of advisory and research work, especially in connexion with the cyst-forming species of *Heterodera*. It is employed for three main purposes: the determination of presence or absence for the issue of so-called certificates of freedom from infection; as a basis for advice on the safety of cultivating susceptible crops on infected land; and for the assessment of soil populations in research. The standards of accuracy required for research are higher than for advisory work. Here, accuracy may have to be sacrificed for expediency and the methods employed judged not so much by scientific appraisal as by reasonable satisfaction with the results achieved.

EXTRACTION OF NEMATODES FROM SOIL

The basis of all soil population estimates is the extraction of nematodes from the soil by water flotation (Morgan, 1925; Goodey, 1951). For the cyst-forming nematodes, the Fenwick can (Fenwick, 1940) represents the greatest advance in technique in recent years and, with the addition of a sludge drain to facilitate clearance between samples, is now in general use in western Europe. Flotation is usually followed by screening through sieves of appropriate mesh. In Bergen-op-Zoom, Holland, this procedure is reversed (Hellinga, 1942), soil containing cysts being first screened on two sieves under a water jet, and the contents of the lower sieve being flushed into a porcelain bowl where flotation occurs. Extraction of nematodes free in the soil is more difficult but may be accomplished by Seinhorst's ingenious apparatus or by that of Oostenbrink, shown in Fig. 1 (Oostenbrink, 1954). The essential difference between this and Fenwick's can is the controlled upward water current employed to separate differentially the nematodes from the light soil particles.

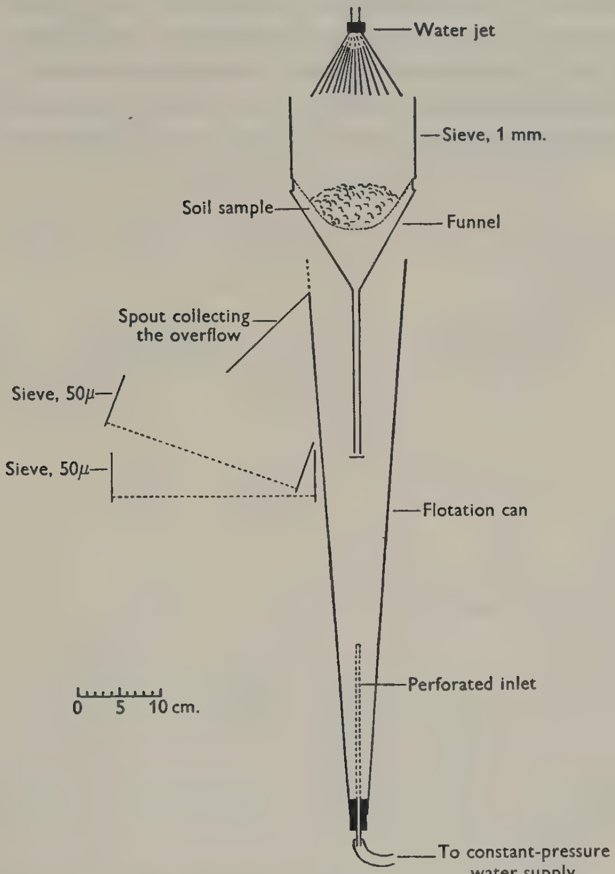
Water jet
Sieve, 1 mm.
Soil sample
Funnel
Spout collecting the overflow
Sieve, 50μ
Sieve, 50μ
Flotation can
Perforated inlet
0 5 10 cm.
To constant-pressure water supply

Fig. 1. Oostenbrink's apparatus for the collection of nematodes free in soil. The soil sample is washed through the upper sieve into the flotation can and the nematodes are separated from the soil by a controlled upward water current introduced from below. (Copied from a drawing supplied by Oostenbrink.)

Enumeration of free nematodes is by direct counting of a fraction of the float. The methods employed for the collection and counting of eelworm cysts are diverse. On the Continent it is customary to transfer the float with water to a porcelain bowl and to collect the cysts from around the rim with a fine brush. In England, filter-papers are preferred or the Fenwick tray is used for larger floats. Buhr (1954) advocates the collection of cysts on filter-paper strips placed directly in a cylindrical flotation vessel, and claims for his method a considerable saving of time.

Whatever method is employed, assuming that it is basically sound, the results of counts from a mixed bulk of soil should fit the Poisson distribution (Fisher, 1938; Simpson & Roe, 1939). From this it follows that the accuracy of a single count is determined solely by its size. Thus if X = the count, then $\sqrt{X}$ = the standard error and the standard error % mean $\left(\frac{100\sqrt{X}}{X}\right)$ is a measure of the degree of accuracy. In Fig. 2 this value is plotted for counts ranging from 1 to 170 and shows the relative inaccuracy of small counts and the rapid increase in accuracy up to counts of about 100. For counts of 10 or more, the Poisson frequency distribution approaches the normal distribution and, therefore, the range including 95% of repeated estimates is given by ± 2 S.E. ($\pm 2\sqrt{X}$). In practice variances obtained from counts are usually in excess of the expected Poisson values because of imperfections in technique (Jones, 1945). Variances consistently less than the expected values are more serious and indicate bias.

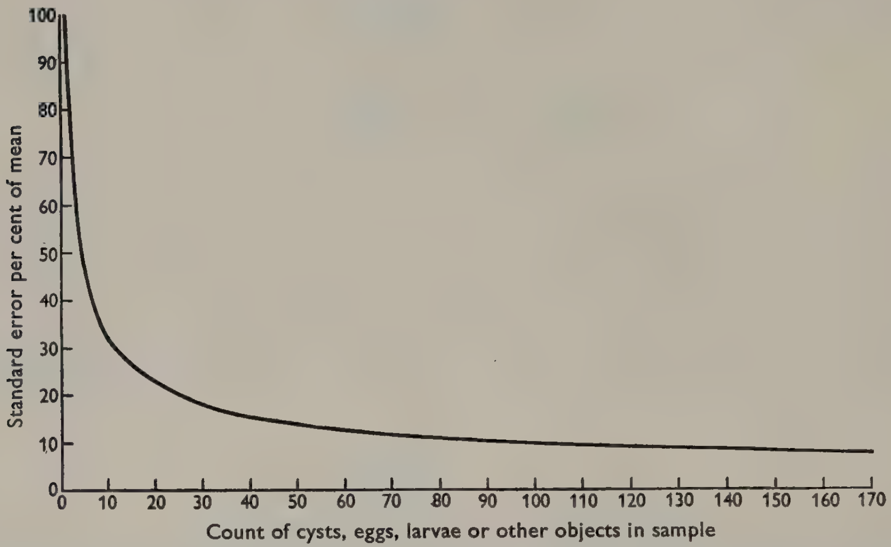

Fig. 2. The relationship between accuracy as measured by standard error per cent of mean and the size of counts from individual subsamples where the counts fit the Poisson distribution.

For low counts such as are encountered in testing for presence or absence in soil or produce certification schemes, Table 1 indicates the difficulties involved. Virtual certainty of detection is not reached until the field population approaches a density of 30–60 × 10^6 eelworms/acre and soils declared 'free' of eelworms may in fact harbour populations up to these substantial levels (Peters, 1951). Inability to measure small populations is also a problem in research and prevents the accurate assessment of rates of increase from low initial levels in the field. Other limitations of soil-sampling techniques for the cyst-forming nematodes arise from failure to extract all cysts, especially those newly formed, from the exclusion of free larvae and external egg masses and the complete disregard of the males.

TABLE 1. *The chances of finding eelworms in soils by means of* 100 *g. soil samples*

			Percentage chances	
Average concentration in field* (per acre)	Concentration per kg. of soil (per 2 lb.)	Expected count per 100 g. sample	of finding one or more cysts (detection)	of finding no cysts (failure)
1 × 10^5	0·1	1 in 100 samples	1	99
1 × 10^6	1	1 in 10 samples	10	90
10 × 10^6	10	1	63	37
20 × 10^6	20	2	85	15
30 × 10^6	30	3	95	5
40 × 10^6	40	4	98	2
50 × 10^6	50	5	99	1
60 × 10^6	60	6	99·9	0·1

* Assuming that there are 1000 tons of top soil or 10^9 g. per acre.

FIELD SAMPLING

For field sampling, it is customary to pool together a number of small samples from the parcel of land under test. In order to form a true picture of the distribution of eelworms, the individual estimation of very many small samples would be necessary (Fenwick, 1952*a*) and the results could be used to construct complex contour maps showing the distribution both superficially and at depth. A transect through a field would produce a graph of the type shown in Fig. 3 in which XY shows the variation in eelworm population from point to point, AB the true mean level of the transect population, A_1B_1 the deviation of the bulk sample mean obtained by pooling a number of small samples taken along the transect, and A_2B_2 the final laboratory estimate from sampling the bulk sample. It is clear that the final estimate of the mean population level may depart from the true mean by a considerable margin, and that it gives no information concerning variability within the field.

Because of dependence upon the Poisson distribution the errors associated with laboratory sampling can be readily assessed. With field sampling the position is less satisfactory. Despite two decades of work in this line, little information is available upon which to decide: (1) the depth of sampling; (2) the size of samples; (3) the number of samples. These factors together determine the quantity of soil in the bulk sample and, the greater this is, the nearer the bulk sample mean approaches the true mean. For advisory work, the determination of the minimum bulk sample size consistent with reasonable accuracy and the best allocation of labour between the factors listed above is highly desirable. For most systems of sampling at present in use there are no estimates of the deviation of the bulk sample mean from the true mean and the only information on within-field variability is that of Anscombe (1950) which relates to a few fields all of rather high population level. Variability within fields tends to decrease as the population rises. A possible reason, therefore, for the success of advisory techniques is the high level of critical populations above which symptoms of eelworm injury appear. Thus, the critical level for potato-root eelworm was estimated by Johnson & Thompson (1945) at 500 × 10^6 cysts with contents/acre and for beet eelworm by Jones (1945) and Goffart (1952) at about 100 × 10^6 cysts with contents/acre.

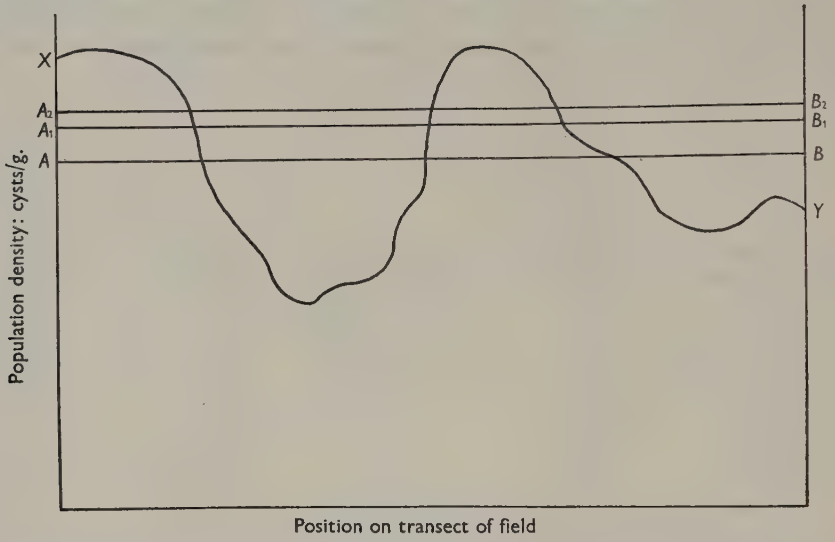

Fig. 3. Diagrammatic representation of the errors of field sampling. *XY*, fluctuations in population along transect through field. *AB*, true mean level of transect population. A_1B_1, mean of bulk sample obtained by combining a number of individual samples taken on transect. A_2B_2, estimate of bulk sample mean obtained in the laboratory.

In research, control of spatial variability is often necessary and may be achieved by using large pots (Peters, 1952) or very small plots (microplots) in which variability in soil population can be eliminated by mixing. A sample of the results obtained from microplots is shown in Fig. 4 in which the initial populations of beet eelworm are plotted against the final populations after growing sugar beet. Over the whole range of initial populations from 2 to 252 hatchable larvae/g. soil the final populations reached a ceiling of about 100 hatchable larvae/g. At 2 larvae/g. this represents a 50-fold increase, at 100 larvae/g. no increase, and at 200 larvae/g. a decrease to half the initial level. Had these microplots represented different parts of the same parcel of land, bulk sampling before and after growing beet would have given only the mean initial level (about 40 larvae/g.) and the general rate of increase (2·5 times), which represents a considerable loss of information.

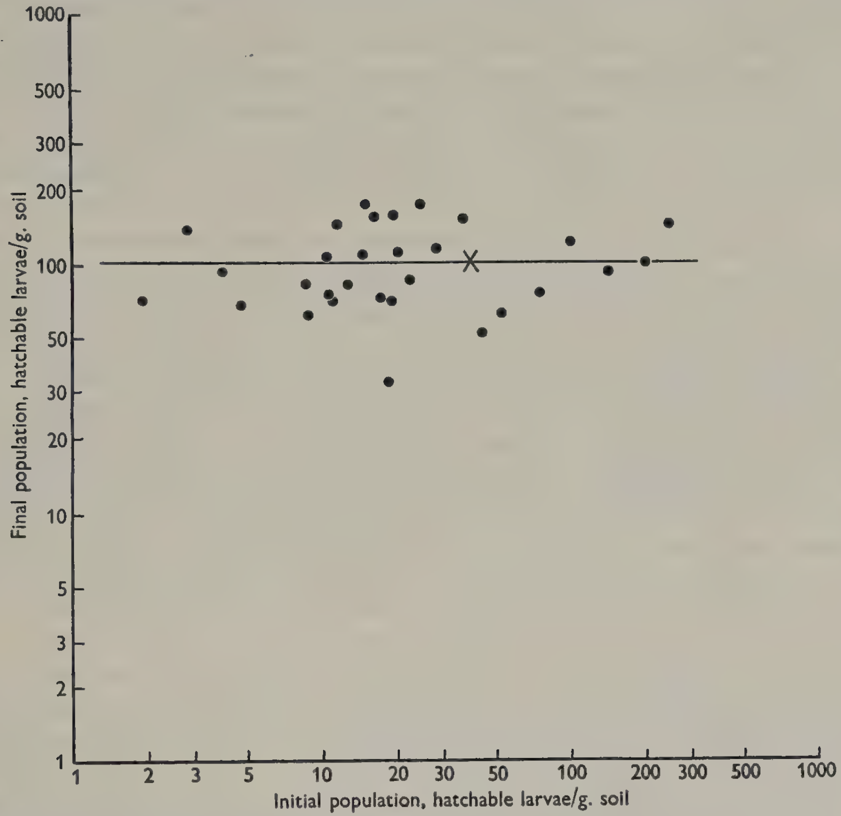

Fig. 4. The results of some microplot experiments with beet eelworm. The relation between initial and final populations of thirty plots sown with sugar beet. Final populations tended to rise to a ceiling level of 100 hatchable larvae/g. soil regardless of the initial level. ●, information from individual plots; ×, information that would have been given by a bulk sample from the same plots.

Assay of cyst contents

Early workers used cyst counts as a measure of the degree of infection of the soil (Morgan, 1925), but it is now recognized that cysts are a better measure of the age rather than the strength of a population. Morgan & Peters (1929) and others commented on the lack of correlation between the cyst content of soils and the development of crop symptoms in the potato crop. Jones (1945) showed that for beet eelworm there was no correlation between cyst counts and egg counts, but that a reasonable correlation existed between cysts with contents ('viable cysts') and eggs. This correlation is the basis of most advisory techniques. It is often coupled with various schemes for the estimation of 'fulness' of cysts (Triffitt, 1934), but these introduce personal errors which make it difficult to equate the techniques of different groups of workers. These difficulties are overcome by estimation of the egg contents of cysts. Petherbridge, Stapley & Thomas (1938) crushed cysts and estimated their egg contents by counting the 'halos' of eggs and larvae around them with the aid of a squared micrometer eye-piece. Oostenbrink (1950) crushed cysts with a thick cover-glass mounted on a handle and estimated the 'halos' by comparison with a set of prepared standards. Techniques of this type give rather variable results in which the final estimate is much too low. An alternative is to crush the cysts between slides and to make up a suspension of the eggs and larvae so liberated. Jones (1945) mixed the suspension by bubbling compressed air through it and, by means of a siphon, forced over drops of known size in which eggs and larvae could be counted. A simpler method is to agitate the suspension by blowing down the pipette used for withdrawing the subsample. Counting is then done by running the subsample into a modified McMaster slide (Fenwick, 1951). A difficulty sometimes encountered with squash techniques is failure of the egg masses to break up or to separate from the cysts. Bijloo (1954) overcomes this difficulty by whizzing the suspension in a homogenizer. Yet another method of estimating cyst contents is the hypochlorite technique of Fenwick (1942, 1952*b*) but this has few advantages over the simple squash technique referred to above. In counting subsamples from well-mixed suspensions, the same statistical principles apply as in the counting of cysts from bulk soil samples. Counts should fit the Poisson distribution and their accuracy is determined solely by their magnitude (Peters, 1941).

None of the techniques for the assay of cyst contents so far described gives a reliable guide to the viability of those contents, which at present can only be accurately assessed by hatching tests conducted in a root diffusate appropriate to the species. The basic principles of the hatching process have been worked out for potato-root eelworm by Fenwick (1949 *et seq.*). Winslow (Jones & Winslow, 1953; Winslow, 1953, 1955) has shown that the same principles hold for several other common species of *Heterodera* and that the use of root diffusates can be extended to the bio-assay of mixtures of cysts of different species. The chief drawback of these tests is the time and labour which they require but this aspect is generally overstressed. Attempts have been made to assess viability by more rapid methods. Thus Boyd (1941) used iodine staining to differentiate living and dead larvae. Homeyer (1953) employed acridine dyes and ultra-violet light to give fluorescent colour differences between living and dead eggs and larvae. Chamberlain (*in litt.*) and Staniland (*in litt.*) have used the appearance of larvae artificially hatched from eggs. Dead larvae are said to remain kinked while living larvae rapidly straighten leaving no trace of the folds caused by coiling within the egg.

Where more detailed information about the pattern of hatching from a cyst population is required, single cyst techniques must be employed, such as used by Gemell (1940), Ellenby (1943), and den Ouden (1954). Owing to the high variability between cysts large numbers of single cyst cultures must be set up, and the interpretation of results is rendered difficult by the high proportion of unproductive cysts. Logarithmic transformation of the data for statistical analysis does not entirely overcome this difficulty.

As will be appreciated, a considerable range of assay techniques are available for the assessment of viability of cyst contents and these may be used not only for estimation of soil populations but also in estimating the strength of root diffusates (Fenwick, 1952*c*) and in investigating the hatching, inhibiting and lethal properties of various chemicals.

ESTIMATION OF EELWORMS ON OR WITHIN PLANTS

Some progress has been made in techniques for the estimation of eelworms found on or within plants. The numbers of nematodes within leaf and stem structures might possibly be estimated by means of Seinhorst's mist apparatus (Seinhorst, 1950). Estimation of cysts adhering to roots has been attempted by Fenwick & Reid (1951), and estimation of the nematodes within roots by Taylor & Loegering (1953). For the latter, washed roots are cut into short lengths and macerated in water in a food homogenizer. This liberates the eelworms which may be screened from most of the plant debris by sieves of suitable mesh. Counting may then be done with the aid of a modified McMaster slide as for egg and larval suspensions. Recognition of the nematodes is facilitated if the roots are first stained in acid fuchsin.

CONCLUSION

Perhaps the greatest need with nematological techniques at present is careful study to see how time and effort may be saved without loss of accuracy. Those newly entering the field upon whom this labour may fall will be greatly helped by an elementary knowledge of statistics and, in particular, by mastery of the implications of the Poisson distribution, which plays more part in present nematological methods than in other branches of biology.

REFERENCES

ANSCOMBE, F. J. (1950). Soil sampling for potato root eelworm cysts. A report presented to the conference of advisory entomologists. *Ann. appl. Biol.* **37**, 286–95.

BIJLOO, J. D. (1954). A new method for estimating the cyst contents of the potato-root eelworm *Heterodera rostochiensis* Wollenweber. *J. Helminth*, **28**, 123–6.

BOYD, A. E. W. (1941). Determination of death in larvae of the potato root eelworm. *Nature, Lond.*, **148**, 782.

BUHR, VON H. (1954). Untersuchungen über den Kartoffelnematoden. 1. Die 'Papierstreifen-Methode', ein vereinfachtes Verfahren zur Untersuchung von Bodenproben auf ihren Besatz mit Nematodenzysten. *NachrBl. dtsch. PflSchDienst, Berl.*, **3**, 1–4.

COBB, N. A. (1918). Estimating the nema population of soil. *Agric. Tech. Circ. U.S. Dep. Agric. Bur. Pl. Ind.* no. **1**, 1–48.

ELLENBY, C. (1943). A modification of the Gemell single cyst technique for the potato strain of the eelworm *Heterodera schachtii* Schmidt. *Nature, Lond.*, **152**, 133.

FENWICK, D. W. (1940). Methods for the recovery and counting of cysts of *Heterodera schachtii* from soil. *J. Helminth.* **18**, 155–72.

FENWICK, D. W. (1942). The degree of *Heterodera* infectivity of soil and its determination. *J. Helminth.* **20**, 50–66.

FENWICK, D. W. (1949). Investigations on the emergence of larvae from cysts of potato-root eelworm *Heterodera rostochiensis*. 1. Technique and variability. *J. Helminth.* **23**, 157–70.

FENWICK, D. W. (1951). A new modification of the McMaster slide for use in potato-root eelworm investigations. *J. Helminth.* **25**, 173–6.

FENWICK, D. W. (1952*a*). Sampling techniques and the limits of their applicability. *Proc. Int. Nemat. Symposium. F.A.O., Rome*, pp. 8–12.

FENWICK, D. W. (1952*b*). The estimation of the cyst contents of potato-root eelworm. *H. rostochiensis*. *J. Helminth.* **26**, 55–68.

FENWICK, D. W. (1952*c*). The bio-assay of potato-root diffusate. *Ann. appl. Biol.* **39**, 457–67.

FENWICK, D. W. & FRANKLIN, M. T. (1942). Identification of *Heterodera* species by larval length. Technique for estimating the constants determining length variations within a given species. *J. Helminth.* **20**, 67–114.

FENWICK, D. W. & FRANKLIN, M. T. (1951). Further studies on the identification of *Heterodera* species by larval length. Estimation of the length parameters for eight species and varieties. *J. Helminth.* **25**, 57–76.

FENWICK, D. W. & REID, E. (1951). A rapid method for estimating the density of white cysts of *Heterodera rostochiensis* on potato roots. *Nature, Lond.*, **167**, 534.

FISHER, R. A. (1938). *Statistical methods for research workers*, 7th ed. Edinburgh: Oliver & Boyd.

GEMELL, A. R. (1940). Studies in the biology and control of *Heterodera schachtii* (Schmidt). (1) Comparison of *H. schachtii* cyst populations from two potato growing districts. *Bull. W. Scot. Agric. Coll.* no. 139, 1–15.

GOFFART, H. (1952). Ansteigen und Abklingen der Nematodenverseuchung und ihre Bewertung im Rübenbau. *Zuckerrübenbau*, **14**, 315–17.

GOODEY, T. (1951). Laboratory methods for work with plant and soil nematodes. *H.M.S.O., Lond., Tech. Bull.* no. 2, 1–25.

HELLINGA, J. J. A. (1942). De invloed van het bietenaaltje op de opbrengst en de samenstelling van suikerbieten. *Meded. Inst. Suikerbiet, Bergen-o.-Z.* **12**, 163–82.

HOMEYER, B. (1953). Die Prüfung von Nematodenmitteln auf fluoreszenzoptischen Wege. *Mitt. biol. ZentAnst. Berl.* **75**, 232–5.

JOHNSON, L. R. & THOMPSON, H. W. (1945). Potato root eelworm in Yorkshire. *J. Minist. Agric.* **52**, 266–70.

JONES, F. G. W. (1945). Soil populations of beet eelworm (*Heterodera schachtii* Schm.) in relation to cropping. *Ann. appl. Biol.* **32**, 351–80.

JONES, F. G. W. & WINSLOW, R. D. (1953). Hatching responses in root eelworms (*Heterodera* spp.). *Nature, Lond.*, **171**, 478.

MORGAN, D. O. (1925). Investigations on eelworm in potatoes in South Lincolnshire. *J. Helminth.* **3**, 185–92.

MORGAN, D. O. & PETERS, B. G. (1929). The potato-root eelworm in Lincolnshire. *J. Helminth.* **7**, 63–80.

OOSTENBRINK, M. (1950). Het aardappelaaltje (*Heterodera rostochiensis* Wollenweber), een gevaarlijke parasiet voor de eenzijdige aardappel-cultuur. *Versl. PlZiekt. Dienst Wageningen*, **115**, 1–230.

Oostenbrink, M. (1954). Een doelmatige methode voor het toetsen van aaltjesbestrijdingsmiddelen in grond, met *Hoplolaimus uniformis* als proefdier. *Meded. LandbHoogesch., Gent* **19**, 377–408.

Ouden, den H. (1954). Het bietencystenaaltje en zijn bestrijding. 1. Methoden te gebruiken bij het onderzoek naar kunstmatige en natuurlijke lokstoffen. *Meded. Inst. Suikerbiet, Bergen-o.-Z.* **24**, 101–21.

Peters, B. G. (1941). Dilution egg counts and the Poisson Series. *J. Helminth.* **19**, 59–62.

Peters, B. G. (1951). The term 'eelworm-free' soil in plant quarantine regulations. *Nature, Lond.*, **167**, 368.

Peters, B. G. (1952). Pot tests of nematicides against potato-root eelworm. 1. Pilot test and methods. *Ann. appl. Biol.* **39**, 447–56.

Petherbridge, F. R., Stapley, J. H. & Thomas, I. (1938). The beet eelworm (*Heterodera schachtii* Schm.). *J. Minist. Agric.* **45**, 226–36.

Seinhorst, J. W. (1950). De betekenis van de toestand van de grond voor het optreden van aantasting door het stengelaatje (*Ditylenchus dipsaci* (Kühn (Filipjev)). *Tydscht. PlZiekt.* **56***e*, 289–349.

Simpson, G. G. & Roe, A. (1939). *Quantitative zoology*, 1st ed. New York: McGraw Book Co. Inc.

Taylor, A. L. & Loegering, W. Q. (1953). Nematodes associated with root lesions in Abaca. *Turrialba*, **3** (N.S.), 8–13.

Triffitt, M. J. (1934). Experiments with the root excretions of grasses as a possible means of eliminating *Heterodera schachtii* from infected soil. *J. Helminth.* **12**, 1–12.

Winslow, R. D. (1953). Hatching responses in some *Heterodera* species. *Ann. appl. Biol.* **40**, 225–6.

Winslow, R. D. (1955). The hatching responses of some root eelworms of the genus *Heterodera*. *Ann. appl. Biol.* **43**, 19–36.

Bovien, Prosper (1955). *Ann. appl. Biol.* **42**, 382–390

HOST SPECIFICITY AND RESISTANCE IN PLANT NEMATODES

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The title of the paper which I shall have the honour to read to-day covers a very wide field as the problems of host specificity and resistance are closely linked up with questions concerning the species concept in plant nematodes.

I hope you will understand that I cannot give an exhaustive review of the literature dealing with the problems but I can try to point out where we stand to-day, what we know and—perhaps even more important—what we should like to know.

The problems of host specificity have been made the subject of discussion by several authors. I shall first mention the important publications by Steiner (1925), Hodson (1926), Quanjer (1927), de Bruin Ouboter (1930) and van Slogteren (1920, 1931) and a paper which Dr Tom Goodey, whom we should have been happy to have among us to-day, read at a meeting of this Association in 1931. He gave on that occasion, a critical survey of the views held by the authors mentioned. He had himself, as early as 1922, published a paper dealing with the susceptibility of various clovers and legumes to a red clover race of *Ditylenchus dipsaci*.

Since 1931 it has been evident that our knowledge of the host range of the various species and races has increased considerably and much important information of scientific, as well as of practical value has been obtained, but nevertheless it does not seem to me that very much advance has been made towards a deeper understanding of the real nature of the so-called biological or physiological races.

The term 'plant nematodes' includes those species which are not only plant feeders but are able to do damage to the plants. Such species have one thing in common: their mouth armature enables them to puncture the surface of the plants, suck out the contents of the cells or penetrate into the internal tissues. Surface damage can be done to the roots as well as to the parts of the plant which are above ground. I hesitate to apply the term ectoparasite to the nematodes which feed externally on roots migrating from place to place. For such vagrant root feeders Steiner has suggested the use of the term 'planosites'. In those species host specificity is not very pronounced, but apparently it is not wholly absent. According to Graham & Holdeman (1953) *Belonolaimus gracilis* is detrimental to cotton and certain other crops but is never found among the roots of tobacco.

Where species which are living above ground in buds, in sheaths and in folded leaves are concerned, I think, however, that we are fully entitled to speak about ectoparasites. Species of *Aphelenchoides* afford good examples. They live in that way for shorter or longer periods, during which multiplication takes place. That some of those species can also live as endoparasites is a remarkable fact. The strawberry eelworms (*A. ritzema-bosi* and *A. fragariae*) are, as we know, chiefly ectoparasitic on strawberries but they can also live as endoparasites in the leaves of chrysanthemum, begonia and other host plants. The host range of these species appears to be rather wide, but they do not attack every plant which is offered to them, so that a certain degree of host specificity exists.

If we return to the species which are surface feeders on roots we know that some of them are able, occasionally, to penetrate deeper into the roots so that their body may be found partly or totally located within the cortex. This is no true parasitism but a transitional stage on the way to the total and obligate parasitism which we find, for example, in the members of the *Pratylenchus* complex. According to Sher & Allen (1953) at least some of the *Pratylenchus* species have different host ranges. In the species of *Pratylenchus* no morphological modifications, according to the parasitic life, are found, but in other Pratylenchinae such as *Tylenchulus semipenetrans*, *Naccobus* spp., *Rotylenchulus reniformis* and *Cacopaurus pestis* the females are plump, swollen or distorted. Some of the species appear to have a limited host range, *Tylenchulus semipenetrans*, for example, being restricted to *Citrus* spp.

When Dr Tom Goodey in 1931 read his paper on 'Biological races in nematodes and their significance in evolution' he first dealt with *Ascaris lumbricoides* as a parasite of man, pig and certain other animals, pointing to the fact that there is strong evidence in favour of the occurrence of biological races in this parasite.

Among the plant parasites he chose *Ditylenchus dipsaci* and *Heterodera schachtii*. As did most workers in those days he regarded the potato eelworm, the sugar-beet eelworm, the oat eelworm etc., as biological strains within the species *H. schachtii*. Later investigations, however, have forced us to change our views on that point. It soon became evident that forms with rounded cysts, *H. rostochiensis* and *H. punctata* were independent species sharply separated from the forms with lemon-shaped cysts. Dr Franklin (1940) found minute morphological differences in the male sex which made it obvious that the sugar-beet eelworm and the oat eelworm were also separate species and had to be named *H. schachtii* and *H. major* respectively. Further investigations carried out in U.S.A., Holland and elsewhere have shown that we have to deal with several more or less well-defined species with lemon-shaped cysts. In some cases, however, we are not yet sure if we have 'good species' or varieties (races) before us. I can, for example, refer to *H. galeopsidis* and *H. trifolii*. In the species of *Heterodera* we find a more or less pronounced host specificity. *H. rostochiensis* appears to have a very narrow host range as it is confined to species belonging to the Solaneaceae. *H. major* is oligophagous too, as it only attacks cereals and grasses. *H. schachtii*, on the other hand, has a wider host range and must be called polyphagous. Among the host plants we find

Chenopodiaceae and Cruciferae, together with some wild and cultivated species belonging to certain other families. Records of infestation on plants other than Chenopodiaceae and the Cruciferae ought, however, to be regarded with suspicion if experimental evidence does not lend support to their reliability.

In Denmark the worst pest as far as cereals are concerned is the oat nematode and the annual losses are very high. Oats, barley and wheat are heavily attacked, whereas the infestations on rye are less important from a practical point of view. Rye is, however, by no means non-susceptible. Some strains of barley have proved to be partially resistant. We find cysts on the roots but there is a considerable difference in number if those strains are compared with other strains generally cultivated in Denmark. This difference manifests itself if oats are sown in the same plots the following year and cyst counts on the roots are performed. We always find the lowest infestation where the partially resistant strains have been grown the preceding year.

The various oat strains are not infested to the same degree but the differences have hitherto been too slight to be of practical value. The work with screening of varieties is, however, still going on. All our fodder-grasses have proved to be susceptible but to a highly varying degree. The work with breeding for resistance against *H. rostochiensis* which is going on in England as well as in Holland and Germany has yielded exceedingly interesting results, which we hope may soon prove to be of practical value too.

What we formerly have been calling *H. marioni* has now, as you all know, appeared to be a taxonomic complex of species or races, which Chitwood (1949) has placed in the genus *Meloidogyne*, but as he says: 'Members of the genus *Meloidogyne* are extremely adaptable and their morphological characters show considerable variation. In fact we have not as yet seen two identical specimens. Nevertheless, general pattern series and other structures show similarities, and progenies from individual females are relatively consistent both as to morphology and host range.'

Although the American workers regard the members of this genus as separate species they have not abandoned the concept of host races within these species. Racial differences are, for example, stated to exist in *Meloidogyne incognita* var. *acrita*. Allen (1952) writes that the data obtained in experiments with cotton populations have made it evident 'that the host range of *M. incognita* var. *acrita* may be subject to considerable within-species variation' and that 'what is true with a species from California is not necessarily true with the same species from some other part of the United States'.

This is important because we meet with the same problem in other plant nematodes and especially in *Ditylenchus dipsaci*. It is further a remarkable fact (as stated by Christie (1949)), that tomato is highly susceptible to several species of *Meloidogyne*. In *Ditylenchus*, too, certain plants can be suitable hosts for populations of various nature and origin.

Can these problems of host specificity and taxonomy in *Meloidogyne* be solved in a satisfactory way? I think that the prospects are rather bright.

Jocelyn Tyler (1933) has proved that propagation in *Meloidogyne* is mainly parthenogenetic and that it is possible to make single-larva inoculations and work with pure lines of the parasites. When clones of the host plant are used, as in the inoculation experiments of Dropkin (1954), it is possible to get reliable information on the variability of the morphological characters and a deeper insight into the problems of host specificity. The Dutch botanists Quanjer and van Slogteren had, many years ago, pointed out the fact that the questions concerning biological races in *Ditylenchus dipsaci* could not be solved in a satisfactory way until the experiments can be performed with pure lines of the parasite as well as of the host plants. This method has thus proved to be applicable in the case of *Meloidogyne*. Before leaving *Meloidogyne* I must draw your attention to a recent publication by Sasser (1954). It contains much important information about susceptibility and resistance in some species belonging to this genus.

Since the eighties of the last century when Ritzema Bos carried out his experimental researches it has been the general view that a considerable number of more or less specialized biological races (or perhaps better host races) occurred within the species *Ditylenchus dipsaci*. They were generally believed to be morphologically indistinguishable, so that identification could only be based on their host relation. Many observations in the fields, as well as the results of numerous infection experiments, lend support to the above-mentioned view. I should like, however, to draw attention to a paper by Dr G. Steiner read at the 14th International Zoological Congress in Copenhagen in 1953. The title was: 'The problem of the taxon in the Nematode genus *Ditylenchus* and its agricultural implications'. Dr Steiner stated that many of the forms which had hitherto been regarded as separate host strains of *D. dipsaci* are distinguishable by minute morphological characters and that he regarded them as good species. This is indeed very interesting! So far as I can see, it is, however, too early to decide if we really have 'good species' in the traditional sense of the term before us. Dr Steiner himself used the term *taxon* (plural *taxa*) in his paper, and I think it was wisely done. The word taxon has recently been created by the botanists to designate what was formerly called a taxonomic category. Before we decide to split up the old species *D. dipsaci* in a number of new species it will be necessary to ascertain if the distinguishing characters are linked to the genotype or are merely the results of environmental influence.

In 1931 van Slogteren pointed to the outstanding researches which Stakman and co-operators had carried out with biological strains of the fungus *Puccinia graminis* and made it evident that the botanists had to deal with similar problems as the plant nematologists, and that the methods used by the mycologists ought also to be applied when plant nematodes are concerned.

Now I hope you will allow me to appear for a moment as an entomologist. Host specificity is an important problem in entomology too, and several workers have dealt with this problem. Among insects we often meet with the same phenomenon which I have just mentioned. We have populations which are almost or wholly indistinguishable morphologically although they differ in respect to host preference. This is, for example, the case in aphids. You all know the cherry blackfly (*Myzus cerasi*). The late German aphidologist Börner (1952) has, however, proved that we have to deal with two forms, one of which lives and feeds on sour cherries, *Prunus cerasus*, and the other on sweet cherries (*P. avium*). The aphids from *P. cerasus* do not go over to *P. avium* and vice versa. According to Börner the populations can be distinguished biometrically but not morphologically. Cross-mating does not occur spontaneously in nature but can be performed in the laboratory. Börner concluded that two independent species (*Myzus cerasi* and *M. pruniavium*) were present on the cherry trees.

Among gall midges we also frequently meet with populations which are almost or totally indistinguishable morphologically. With respect to biology and host range they may, however, behave in a very different way and I can advise you to consult a paper which Dr H. F. Barnes (1953) published recently. The title is: 'The biological approach to the species problem in gall midges'. Dr Barnes writes: 'While evidence is accumulating so rapidly no attempt has been made in this paper to assess or define the limitations of "species", "races", "strains", etc.' He considers it to be a purely academic question if we have to call an insect a 'species' or a 'physiological race'. We have thus among insects populations which are so closely related that, just as where plant nematodes are concerned, we are entitled to speak about taxonomic groups or complexes which, as Barnes says, are still in the course of evolution. He also writes that 'it is plausible to suggest that the physiological adaptations necessary for life on the sap of a new host plant would arise long before their reflexion in the insect's morphology'. This, I believe, holds true for nematodes too. Many other examples could be found within other groups of insects (Coccids, Hymenoptera, Diptera, etc.) and also among the mites (e.g. the *Bryobia praetiosa* complex).

We must now return to the plant nematodes and ask ourselves the question: 'What can we do to get a deeper insight into the problems connected with their taxonomy and host specificity?' Let us turn our attention to *Ditylenchus dipsaci*. What do we want to know? We want to know if the minute morphological differences which Dr Steiner no doubt will soon tell us more about are constant and not due to host-determined variation. Furthermore, we want to know if interbreeding takes place within mixed populations and if fertile hybrids are produced. It will be very difficult to solve these problems and new methods of approach must be found. Innumerable inoculation experiments have been performed and, as you know, the results have often been highly diverging, the explanation no doubt being that the populations used have not been of the same genetic character. The fact that one host plant can harbour individuals which are representing different strains is a further danger! Single-larva inoculations cannot be applied, as in *Meloidogyne*, because *Ditylenchus* is not (at least as far as we know) parthenogenetic. It might, however, be possible to select pre-adult individuals of one race and apply them singly to isolated seedlings. A certain percentage of them would penetrate the seedlings, undergo the last ecdysis and manifest their sex. The females could then be selected and used as an inoculum together with males of the other race in question. To perform such experiments would, however, be a strenuous task as it would be necessary to work with numerous individuals and seedlings. I do not know if the method is practicable.

It would be a great advantage if a method could be found enabling one to cultivate *D. dipsaci* on an artificial medium. This method has been found to be applicable to certain species of *Aphelenchoides* and to members of the *Ditylenchus destructor* complex, but nobody has yet succeeded in cultivating *D. dipsaci*, which is a more pronounced parasite than, for example, *D. destructor* which appears to feed mainly on fungi.

What do we mean when we use the terms susceptibility and resistance (non-susceptibility)? I think the question must be answered in the following way. When the nematodes are able to invade the tissues of the plant and establish themselves, and when the majority of them can reach full sexual maturity (as in *Heterodera*) or multiply and produce successive generations without decrease in number (as in *Ditylenchus dipsaci* and species of *Aphelenchoides*), then the plant is susceptible provided, however, that such symptoms which may be specific to the attack are developed as a result of the presence of the parasite. The last criterion is especially important where *Ditylenchus dipsaci* and species of *Aphelenchoides* are concerned.

If these conditions are not fulfilled then we say that the plant is resistant (non-susceptible). We cannot, however, in all cases draw a sharp line between those two categories as we often meet with partial susceptibility or resistance.

As to the causes of resistance I think that Christie (1949) is right when he says: 'We must recognize the possibility that all resistant plants are not necessarily resistant for the same reason.'

We can take it for granted that there are many cases where resistance is due to the fact that the plant is not at all attractive to the nematodes. The plant is not invaded at all. In other cases, for example where species of *Heterodera* and *Meloidogyne* are concerned, the roots of resistant or partially resistant plants are generally invaded by larvae and often by just as many larvae as susceptible species or varieties. They fail, however, to establish themselves and they cannot reach sexual maturity in totally resistant plants. In plants which are partially resistant only a certain percentage will reach maturity. In *Ditylenchus dipsaci* we find much the same situation.

With regard to these nematodes it also holds true that the parasites do not invade any plant which is being exposed to attack but that they often invade plants which are not suitable hosts. They may live there for a shorter or longer period even multiplying slowly and perhaps producing slight pathological symptoms.

I can mention an example from my own experience. Seedlings of red clover sown on a moist layer of cotton in Petri dishes had a suspension of *D. dipsaci* from *Narcissus* poured over them. A week later twenty seedlings were dissected. A total of 163 eelworms were found in these plants. All seedlings harboured nematodes (up to 50 in each of them). Only one seedling was very slightly deformed, but small necrotic areas were found in or on all plants. Further examination gave the result that pre-adult larvae had reached the adult stage, but no propagation took place. Thus red clover proved *in this case* to be resistant to *Ditylenchus* from *Narcissus*.

If, for example, lucerne seedlings are exposed to infection with *Ditylenchus dipsaci* from red clover then a certain percentage of the seedlings will exhibit the characteristic swellings, whereas the majority will remain normal, even if they are invaded by nematodes. The infection will only persist to a certain extent. The propagation will be slow and the population decrease in number and the symptoms will generally disappear gradually as the plants are growing. In Denmark we regard lucerne as fairly resistant to red clover nematodes, but as pointed out by Frandsen (1951) it is highly possible that certain populations of red clover nematodes have a greater tendency than others to attack lucerne. My own observations in the laboratory, as well as in the field, are supporting his views.

We may thus have populations of diverging genetic character, but it ought not to be forgotten that mixed (sympatric) populations may exist in the fields where various crops (as, for example, red clover, white clover and lucerne) have been grown, either in mixture or separately, in the course of the years.

What I have said about the red clover eelworms and lucerne also applies to two other strains which are important in Denmark, the white clover strain and the lucerne strain in relation to their reciprocal hosts.

The investigations on variation of resistance in red clover and white clover strains have given promising results—perhaps the best results as yet achieved in resistance breeding and screening of varieties! I shall only refer to the publications by Bingefors (1950, 1951), and Frandsen (1949, 1951).

Which factors induce the nematodes to invade the plants? We are rather well informed where species of *Heterodera* and especially *H. schachtii* and *H. rostochiensis* are concerned. German workers have, about 30 years ago, pointed out that what we now call root diffusates stimulate hatching and possess attractive properties. This pioneer work has been continued by a succession of English workers and with highly interesting results.

As a result of the investigations carried out by chemists in Cambridge we have even got some information about the chemical nature of the root diffusates.

We must also assume that certain chemical stimulants play a part when nematodes such as *Ditylenchus dipsaci* and species of *Aphelenchoides* etc. penetrate into the plants. We must suppose that such nematodes respond to stimuli just as the larvae *Heterodera*. At the present moment, however, we know nothing for certain.

The next problem is why the larvae after having invaded the tissues are able to develop into sexually mature adults or multiply in some plants but not in others. Are some chemical constituents decisive? Is it not natural to believe that the presence or absence of certain 'feeding stimulants' (if we are allowed to use this term) may be of importance? Future investigations must solve this problem. We know, however, that it is of vital importance to species of *Heterodera* and *Meloidogyne* that the roots respond to the invasion by the production of giant cells. Barrons (1939) who worked with root-knot nematodes has set forth an interesting 'speculative hypothesis' which reads as follows: 'Resistance may be due to certain chemicals within the roots of resistant plants that counteract or neutralize the giant-cell-inducing effect of salivary secretions of the nematodes.'

I think it is natural to assume that the reactions of the tissues and the subsequent gall-formations in plants attacked by *Ditylenchus dipsaci* are of importance to this parasite too.

We have thus good reason to suppose that chemotactic responses are the prevalent factors that determine host specificity in plant nematodes, but it is possible that morphological differences in the plants may also be of some importance.

I shall now finish this—perhaps rather elementary—lecture in which I have tried to touch some of the problems connected with host specificity and resistance in plant nematodes and I hope you will agree with me when I stress the necessity of finding new methods of approach.

Van Slogteren, whose name I have mentioned several times, advised the plant nematologists to collaborate with geneticists. May I on my own account add, cytologists and biochemists too!

REFERENCES

Allen, M. V. (1952). Observations on the genus *Meloidogyne* Goeldi, 1887. *Proc. Helminth. Soc. Wash.* **19**, 44–51.

Barnes, H. F. (1953). The biological approach to the species problem in gall midges (Dipt., Cecidomyidae). *Ann. ent. fenn.* **19**, 1–24.

Barrons, K. C. (1939). Studies of the nature of root knot resistance. *J. agric. Res.* **58**, 263–72.

Bingefors, S. (1950). Undersökningar över klövernematodens udbredning och förutsättningarna för resistensförädling av rödklöver i mellersta och norra Sverige. *Sverig. Utsädesfören. Tidskr.* **89**, 154–89, 245–76.

Bingefors, S. (1951). The nature of resistance to stem nematode, *Ditylenchus dipsaci* (Kühn) Filipjev, in red clover, *Trifolium pratense* L. *Acta Agric. Scandinavica,* **1**, 180–9.

Börner, C. (1952). *Die Blattläuse Mitteleuropas.* Weimar.

Chitwood, B. G. (1949). Root-knot nematodes. 1. A revision of the genus *Meloidogyne* Goeldi, 1887. *Proc. Helminth. Soc. Wash.* **16**, 2.

Christie, J. R. (1949). Host-parasite relationships of the root-knot nematodes, *Meloidogyne* spp. III. The nature of resistance in plants to root knot. *Proc. Helminth. Soc. Wash.* **16**, 2.

Dropkin, V. H. (1954). Infectivity and gall size in tomato and cucumber seedlings infected with *Meloidogyne incognita* var. *acrita* (root-knot nematode). *Phytopathology.* **44**, 43–9.

Frandsen, K. J. (1949). Breeding of resistant clover in Scandinavia. *Fifth International Grassland Congress,* pp. 1–8.

FRANDSEN, K. J. (1951). Studies on the clover stem nematode (*Tylenchus dipsaci* Kühn). *Acta Agric. Scandinavica*, **1**, 3, 203–70.

FRANKLIN, MARY T. (1940). On the specific status of the so-called biological strains of *Heterodera schachtii* Schmidt. *J. Helminth.* **18**, 193–208.

GOODEY, T. (1922). On the susceptibility of clover and some other legumes to stem disease. caused by the eelworm. *Tylenchus dipsaci* syn. *devastatrix* Kühn. *J. agric. Sci.* **12**, 20–30.

GOODEY, T. (1931). Biological races in nematodes and their significance in evolution. *Ann. appl. Biol.* **18**, 414–9.

GRAHAM, T. W. & HOLDEMAN, Q. L. (1953). The sting nematode *Belonolaimus gracilis* Steiner: a parasite on cotton and other crops in South Carolina. *Phytopathology* **43**, 434–9.

HODSON, W. E. H. (1926). Observations on the biology of *Tylenchus dipsaci* Kühn, and on the occurrence of biologic strains of the nematode. *Ann. appl. Biol.* **13**, 219–28.

OUBOTER, M. P. DE BRUIN (1930). *Tylenchus devastatrix* Kühn uit Narcis en Hyacinth. *Tijdschr. PlZiekt.* **36**, 125–228.

QUANJER, H. M. (1927). Een aaltjesziekte van de aardappelplant, de aantastingswijze en de herkomst van haar oorzak, *Tylenchus dipsaci* Kühn. *Tijdschr. PlZiekt.* **33**, 137–72.

SASSER, J. N. (1954). Identification and host-parasite relationship of certain root-knot nematodes. *Univ. of Maryland Tech. Bull.* no. A 77.

SHER, S. A. & ALLEN, M. W. (1953). Revision of the genus *Pratylenchus* (Nematoda: *Tylenchidae*). *Univ. Calif. Publ. Zoöl.* no. 57, 441–70.

VAN SLOGTEREN, E. (1920). Bestrijding in de Bloembollstreek. *Tijdschr. PlZiekt.* **26**, 126.

VAN SLOGTEREN, E. (1931). Biologiese rassen. *Tijdschr. PlZiekt.* **37**, 137–49.

STEINER, G. (1925). The problem of host selection and host specialization of certain plant-infesting Nemas and its application in the study of nemic pests. *Phytopathology* **15**, 499.

TYLER, JOCELYN (1933). Reproduction without males in aseptic root culture of the root-knot nematode. *Hilgardia*, **7**, 373–88.

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3–5	Soil-borne diseases: eye spot and take-all of wheat	Mary D. Glynne. Rothamsted Experimental Station
4A	Soil moisture gradients and root development in seedlings of Scots pine and Sitka spruce	K. A. Stedman. Imperial College
5A	A method of impregnating soil with synthetic plastic resins	R. N. Jackson. University College, Ibadan, Nigeria
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117, 119	Examples of fumigation for plant quarantine: (1) potato tuber moth; (2) azalea leaf miner	O. F. Lubatti and D. Griffin. Imperial College
146	‘Aroclor’ group of resins	Monsanto Chemicals Ltd. Fulmer, Bucks
147	Development of organophosphorics of low mammalian toxicity, including Diazinon	The Geigy Co., Manchester
151	Development of a range of products, taking BHC as an example	E. Holmes. Plant Protection Ltd., Fernhurst

Jubilee Conference: Summary of programme

JUBILEE CONFERENCE

SUMMARY OF PROGRAMME

(*Note.* Titles of lectures are listed under Contents, pp. v–vii)

Monday, 13 September

11 a.m. Opening meeting, Jehanghir Hall, Imperial Institute

Address of welcome by the PRESIDENT

Replies by Dr K. STARR CHESTER and Dr E. GRAM

Inaugural address by Sir JOHN RUSSELL

2–4 p.m. Symposia held at Imperial College

1*a*. *International co-operation in the field of crop protection*

Chairman: Mr C. T. GIMINGHAM

Speakers: Mr W. C. MOORE, Dr V. E. WILKINS, Dr E. GRAM

1*b*. *Insect pests of stored products*

Chairman: Emer. Prof. J. W. MUNRO

Speakers: Mr F. W. CANN, Mr. D. W. HALL, Dr E. A. PARKIN

5 p.m. Lecture by Emer. Prof. E. C. STAKMAN (Chairman: the PRESIDENT)

8 p.m. Reception by the President and Vice-Presidents at Ayrton Hall

Tuesday, 14 September

10 a.m.–12.30 p.m. Symposia held at Imperial College

2*a*. *Plant viruses and virus diseases*

Chairman: Mr G. G. SAMUEL

Speakers: Dr K. M. SMITH, Prof. E. VAN SLOGTEREN, Dr F. O. HOLMES, Mr F. C. BAWDEN

2*b*. *Plant growth-regulating substances*

Chairman: Dr T. SWARBRICK

Speakers: Prof. R. L. WAIN, Prof. H. BURSTRÖM, Dr W. G. TEMPLEMAN, Prof. L. J. AUDUS

Tuesday, 14 September (*cont.*)

2–4 p.m.

3*a*. *Problems in applied zoology*
Chairman: Prof. H. W. Miles
Speakers: Dr J. Carmichael, Dr T. H. C. Taylor, Prof. J. B. Cragg

3*b*. *Soil-borne pests and diseases*
Chairman: Mr A. Roebuck
Speakers: Dr S. D. Garrett, Dr J. Rishbeth, Dr Ir J. Doeksen

5 p.m. Lecture by Prof. V. B. Wigglesworth (Chairman: Prof. A. E. Muskett)

6.30–10 p.m. Conversazione

Wednesday, 15 September

10 a.m.–12.30 p.m. Symposia held at Imperial College

4*a*. *Education and extension services in applied biology*
Chairman: Prof. R. H. Stoughton
Speakers: Dr L. M. Kramer, Emer. Prof. W. Brown, Sir William Slater, Mr R. Rae

4*b*. *Crop protection*
Chairman: Dr J. T. Martin
Speakers: Dr H. Martin, Dr A. E. Dimond, Dr W. E. Ripper, Dr E. Holmes

2–4 p.m.

5*a*. *Forecasting and assessment of plant diseases*
Chairman: Prof. P. H. Gregory
Speakers: Dr K. Starr Chester, Mr E. C. Large, Mr D. Hille Ris Lambers

5*b*. *Plant nematodes*
Chairman: Dr I. Thomas
Speakers: Dr B. G. Peters, Mr F. G. W. Jones, Dr P. Bovien

5 p.m. Lecture by Dr K. W. Neatby (Chairman: Mr R. W. Marsh)

7.30 p.m. Conference dinner at Ayrton Hall

Thursday, 16 September

Excursions to the following research stations:

East Malling Research Station

Royal Horticultural Society's Gardens, Wisley

Imperial College Field Station, Sunninghill

Wye College (University of London Faculty of Agriculture and Horticulture)

National Agricultural Advisory Service Sub-centre, Wye

Hawthorndale Laboratories, Jealott's Hill Research Station, Bracknell (Imperial Chemical Industries Ltd.)

John Innes Horticultural Institution, Bayfordbury

Butterwick Research Laboratories, Welwyn (Imperial Chemical Industries Ltd.)

Friday, 17 September

Excursions to the following research stations:

National Institute of Agricultural Botany, Cambridge

Plant Breeding Institute, Cambridge

Agricultural Research Council Plant Virus Research Unit, Cambridge

Agricultural Research Council Insect Physiology Unit, Cambridge

Rothamsted Experimental Station, Harpenden

National Vegetable Research Station, Wellesbourne, Warwick

Chesterford Park Research Station, Saffron Walden (Fisons Pest Control Ltd.)—followed by a Dinner in the Hall of Sidney Sussex College, Cambridge

University of Oxford Department of Agriculture

Agricultural Research Council Unit of Experimental Agronomy, Oxford

Hope Department of Entomology, University of Oxford

Imperial Forestry Institute, Oxford

Tilgate Research Station, Crawley (F. W. Berk and Co. Ltd.)—followed by a Dinner at Tilgate.

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EDITORIAL NOTE

In the preparation of this Jubilee Volume some departures from the normal usages of the *Annals* have been necessary. These usages will be resumed in subsequent volumes.